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7401

The Diverse Patterns of Metamorphosis in Gonostomatid Fishes – An Aid to Classification

E. H. Ahlstrom

The gonostomatid lightfishes rank second only to myctophid lanternfishes in abundance in the sea. The gonostomatid genus *Cyclothone* has been singled out as the most abundant group of fishes in the ocean. These observations were based on abundance of adults in mid-water trawl hauls. If abundance is based on larvae, the gonostomatid genus *Vinciguerria* could be the most numerous group of fishes in the ocean. Without attempting to decide whether *Cyclothone* or *Vinciguerria* ranks first in abundance, we can assume that the gonostomatids obviously are an important group of oceanic fishes.

Grey (1964), in her impressive contribution on gonostomatid fishes, recognized 21 genera as valid, with between 52 to 55 valid species. A few species subsequently have been added and a few synonymized, bringing the number of species close to 60. Weitzman (in press) will reduce the number of genera to 20 (pers. comm.). The Gonostomatidae are closely related to the hatchetfishes, family Sternoptychidae; the most recent review of the latter family was made by Baird (1971).

Life histories have been published for 12 of the 20 genera of gonostomatid fishes and for slightly more than a third of the species. In addition to the published record I have larval series for an additional 3 genera and 9 species.

The larvae of Gonostomatidae constitute a moderately homogeneous group. By this I mean that it is not difficult to identify larvae to the family level despite differences noted below. About half the known gonostomatid larvae have moderate to fairly heavy pigmentation that aids in identification. The gut (digestive tract) is more variable in length between larvae of different genera of gonostomatids than perhaps any other family of fishes. It ranges from fairly short, as in *Danaphos*, to a full 95% of the standard length, as visable in an interesting *Maurolicine* larva I will discuss later; occasionally the gut can be trailing, as in *Ichthyococcus*. Gut length is even shorter in the sternoptychid genus *Sternoptyx*. Eyes in larvae are either round or narrowed; but when narrowed they lack the specializations found in the eyes of various myctophid larvae. The most strikingly narrowed larval eyes are found in the sternoptychid genus *Argyropelecus*.

The anal fin in gonostomatids is usually long, occupying most of the tail portion of the body. The shorter dorsal fin, however, is variously placed in relation to the anal. It may completely precede the anal, as in *Danaphos* or *Woodsia*; it may partly precede the anal as in *Vinciguerria* or *Maurolicus*; the origin of the dorsal may be opposite the origin of the anal as in *Cyclothone*; or the anal origin may precede the dorsal by several rays, as in *Gonostoma* or *Araiophos*. In the majority of gonostomatid larvae the dorsal and the anal fins form in about the same relative positions they will retain in later life - but there are interesting exceptions. These are associated with larval forms with relatively long intestines in which the anus shifts anteriorward during metamorphosis, as does the anal fin relative to the dorsal.

Grey (1964) illustrated such a shift in *Pollichthys mauli*, and a marked shift must occur in an interesting *maurolicine* larva that is discussed later.

The caudal fin of gonostomatids is interesting in several respects. The principal caudal rays are invariably 19, a character shared with most salmoniform fishes. The bones that support the principal rays, however, can retain the primitive complement of 4 superior and 3 inferior hypurals as in *Gonostoma* or *Diplophos*, be variously reduced as in *Vinciguerria* (3 + 2) or *Danaphos* (3 + 1) to only 1 superior and 1 inferior hypural as in *Cyclothone* or *Araiophos*, or achieve the ultimate reduction to a single plate in the sternoptychid genus *Sternoptyx*. Similarly epurals can retain the primitive complement of 3, or be variously reduced to none. In no other group of fishes has such a variable pattern of reduction of caudal supporting bones been observed. In the 6 other stomiatoid families of fishes, for example, hypurals are stabilized at 3 superior and 3 inferior plates. In most fishes the procurrent C rays are about equal in number, both in the dorsal group and in the ventral, but in various gonostomatids-sternoptychids the ventral group is reduced in number of rays relative to the dorsal - obviously to accommodate the posteriormost photophores of the AC group. Among the genera with a reduced ventral complement of procurrent caudal rays are *Vinciguerria, Polymetme, Maurolicus, Danaphos,* and *Argyropelecus*; among the genera in which no such reduction occurs are *Cyclothone, Diplophos, Araiophos*, and *Sternoptyx*.

Although larvae of gonostomatids and sternoptychids exhibit marked variability in certain characteristics such as gut length, eye shape, pigmentation and fin position, none of these is of primary value in tracing relationships among genera and species. The patterns of photophore development, during the larval and metamorphic stages and specialization in photophore groups in adults, constitute the most trenchant characteristics for showing such relationships. The notations used to designate photophores follow Grey (1964), with the exception that her IV group is divided into IP + PV groups.

Before discussing photophore information in larval and metamorphic stages, I will briefly characterize photophore groups in adults. Most photophores in gonostomatids are in a ventral series usually extending along the length of the body from symphysis to base of caudal. In addition, photophores are present between branchiostegal rays (6 or more pairs per side), on the head and operculum (3 to 5 pairs), and usually a lateral body series (occasionally several lateral series). In the majority of gonostomatid genera (13) all photophores remain individually separate, but in the other 7 genera some or most of the photophores can be variously clustered into groups with common bases. A similar pattern of clustered photophores is found in the 3 sternoptychid genera.

In most families of stomiatoid fishes, photophores form simultaneously during a relatively brief metamorphic period. They form initially as unpigmented organs and subsequently acquire pigment and structure. This is the pattern of formation, for example, in the families Stomiatidae, Chauliodontidae, Melanostomiatidae, etc.; it is also found in some genera of gonostomatids.

In several genera of gonostomatids, for example *Vinciguerria* and *Cyclothone*, most photophores are laid down initially during a white photophore stage, and only a few photophores are late forming. More commonly, most ventral photophores form simultaneously during a white photophore stage; the lateral photophores form later and usually gradually.

This is the situation in *Ichthyococcus*, *Pollichthys*, and *Diplophos*. All genera with clustered photophores and at least three genera with single photophores (*Gonostoma*, *Margrethia*, and *Bonapartia*) have a protracted metamorphosis with gradual formation of photophores. Even when photophore formation is gradual, each addition is initially unpigmented and then becomes pigmented. Recent additions among pigmented photophores are usually smaller than those formed earlier, hence easily recognized.

The sequence of photophore formation has been as well documented for *Vinciguerria* as for any gonostomatid genus. Developmental series have been described for the 4 recognized species. Sanzo (1913b) showed from life-history studies that 2 species of *Vinciguerria* in the Mediterranean could be distinguished as larvae - *V. attenuata* and *V. poweriae*. Jespersen and Taning (1926) provided additional life-history information for these species and for *V. nimbaria* (as *V. sanzoi*). Ahlstrom and Counts (1958) described the life history of *V. lucetia* and provided information on *V. nimbaria* and *V. poweriae* from the eastern North Pacific; Silas and George (1969) provided additional information concerning development of *V. nimbaria*. The developmental pattern of all 4 species is strikingly similar.

At first formation, photophores are colorless in *Vinciguerria*, but they soon become pigmented. Most photophores appear simultaneously except for 3 to 7 pairs (Fig. 1A).

In *V. lucetia* the late-forming photophores are invariably the following:

A. The upper opercular pair of photophores.
B. The symphysial pair under the lower jaw.
C. A median pair of photophores of the AC group.
D. Two to 4 pairs of lateral photophores of the posterior lateral group.

Only 2 of the 4 recognized species of *Vinciguerria* develop a symphysial pair of photophores; except for this, the late-forming photophores in all 4 species are as listed above, the number of late-forming lateral photophores is reduced to 1 or 2 pairs in *V. poweriae*.

Even though the metamorphic period is relatively short in *Vinciguerria*, Ahlstrom and Counts (1958) indicated a natural division into 3 stages: 1. pro-metamorphosis, the white photophore stage, 2. mid-metamorphosis, when marked changes in body form occur in addition to the development of photophores into functional organs and the formation of several late-forming photophores, and 3. post-metamorphosis during which photophores formation is completed and juvenile body form attained. All stages are commonly taken together in plankton haul sampling no deeper than 200 m.

In *Cyclothone*, all ventral photophores are laid down simultaneously as white stage photophores, and on some species most lateral photophores as well. Developmental series have been described for two species of *Cyclothone*, *C. braueri*, and *C. pygmaea* by Jespersen and Taning (1926) and possibly *C. atraria* (Mukhacheva, 1964 as *C. microdon*). In addition we have developmental series for *C. acclinidens*, *C. signata*, and *C. alba*. Body form and pigmentation are strikingly similar in *Cyclothone* larvae of the various species, which complicates establishing life-history series in this most speciose of gonostomatid genera. Adult taxonomy has recently been clarified by Mukhacheva (1964) and Kobayashi (1973); 12 species are now recognized. Larvae of *Cyclothone* are rather shallowly distributed - i.e. they occur principally in the upper mixed

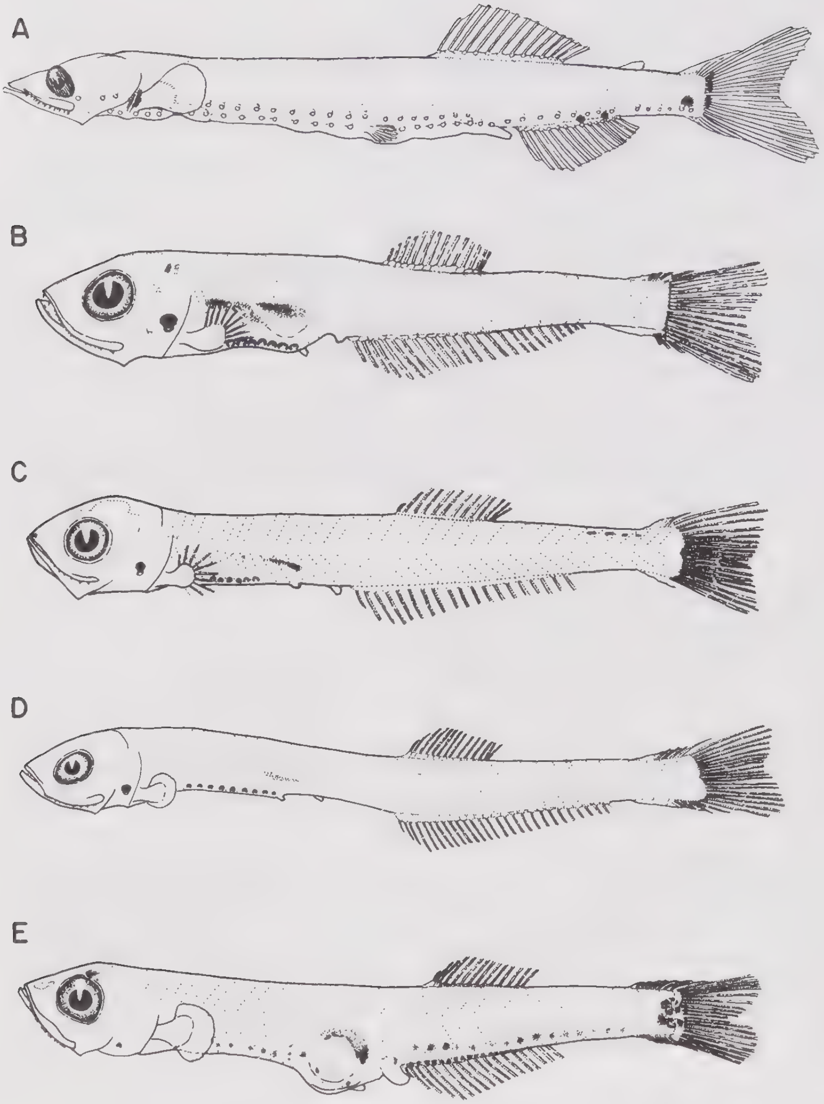

Fig. 1. Larvae and metamorphosing specimens of gonostomatids. (A) *Vinciguerria lucetia*, 15.0 mm, pro-metamorphic stage (from Ahlstrom and Counts, 1958). (B) *Gonostoma elongatum*, 9.8 mm, early metamorphosis. (C) *G. bathyphilum*, 11.0 mm, early metamorphosis. (D) *G. ebelingi*, 15.0 mm, early metamorphosis. (E) *G. atlanticum*, 12.0 mm, late larva

layer (Ahlstrom, 1959) and remain in this depth zone through the pro-metamorphic or white stage of photophore formation; they move to deeper levels to complete photophore formation. Later metamorphic stage specimens of *Cyclothone* are never taken in plankton collections made within the upper 200 m. It should be emphasized that the white photophore stage in *Cyclothone* is strikingly similar to that observed in *Vinciguerria.*

Larvae of *Ichthyococcus* develop more specialized larval characteristics than other gonostomatids, including an elongated ray on the lower part of the pectoral, reminiscent of similar pectoral development on larvae of the myctophids *Loweina* and *Tarletonbeania* (Moser and Ahlstrom, 1970), and a trailing gut. Information on the number of photophore formed initially in *Ichthyococcus* is somewhat inconsistent among authors (Sanzo, 1913a, 1930; Jespersen and Taning, 1926; Grey, 1964) but most photophores of the ventral group form simultaneously as unpigmented "white" photophores, whereas the lateral series forms latter. A 20.3 mm pro-metamorphic specimen of *I. ovatus* collected near Hawaii had 12 BR (definitive), 8 IP (definitive), 17 PV (definitive), 9 VAV (definitive), and 8 + 3 AC (1 or 2 lacking) and no lateral photophores. The AC photophores were divided into 2 groups, a larger anterior group and a posterior group of 3, with 1 or 2 photophores lacking between the 2 groups. A mid-metamorphic specimen illustrated in Jespersen and Taning (1926) has a less complete series of AC (7 + 3), although 13 pairs were developed in the lateral series. Jespersen and Taning indicated that the last photophores to form were the upper OP, posterior photophores of the lateral series, and AC photophores between the anterior and posterior groups. Marked changes in body proportions, particularly a striking increase in body depth, occur during metamorphosis of *Ichthyococcus.* Although metamorphosis is more gradual than in *Vinciguerria* or *Cyclothone*, it is basically similar.

Grey (1964, Fig. 28) illustrates 2 metamorphic-stage specimens of *Pollichthys mauli* of about equal size (16-17 mm), but at different stages of development. At first, I found these illustrations disturbing. The termination of the gut and origin of the anal fin appeared to be too far back on the body on the larger but less advanced specimen. I now know the reason for this: in various gonostomatids the gut length (i.e. snout – anus length) shortens during metamorphosis and in some the origin of the anal fin moves forward relative to the origin of the dorsal fin. This was happening in *Pollichthys* between the 2 metamorphic stages illustrated by Grey.

A less complete complement of photophores is laid down initially than in the preceding genera. Not only is the lateral group of photophores late forming, but the ventral AC group is less complete. The pattern of AC development is strikingly similar to the patterns to be discussed for *Gonostoma* and *Margrethia.* The two posterior AC photophores develop independently of the main group of AC photophores; in the latter the middle photophores develop initially and are added to both anteriorly and posteriorly until the complete complement is formed. The more advanced stage illustrated by Grey has the ventral and head photophores complete, but has only 6 of the lateral group of photophores which will number 19-21 when complete. I have examined post-metamorphic stage specimens of *Pollichthys*, but not the earlier metamorphic stages.

Diplophos has the most elongate larva among gonostomatids, and attains the largest size before transformation (ca. 45-50 mm). Developmental stages of *D. taenia* were described by Jespersen and Taning (1919). Although the majority of ventral photophores form simultaneously in *Diplophos taenia,* few series are actually complete. For example, on a 44.2 mm transforming specimen, the isthmal photophores were incomplete anteriorly, the anterior VAV photophore was small and barely formed; posterior AC group was incomplete. However, the two posteriormost photophores of the AC group were well formed and separate from the main group of AC photophores. The lateral series was partly formed, 25 + 8 photophores, but several anterior photophores were lacking as well as most photophores above the VAV and AC ventral groups. One photophore of the lateral midline group was formed - the posteriormost photophore of this group, which forms far out on the caudal fin (about 2 mm from the caudal base). A 46 mm specimen had midline photophores formed (87 + 1) but still lacked posterior photophores in the lateral group. Even on juveniles this lateral series is often incomplete.

A developmental feature shared by the above genera is that most or all ventral photophores form simultaneously as white stage photophores. In none of these genera are all photophores formed initially, but the number of late-forming photophores are usually the following: OA series of lateral photophores of which some or all are late-forming; AC (anal-caudal ventral series) which usually form as 2 separate groups with 1 to several photophores lacking (*Cyclothone*, an exception); OP photophores, of which the upper pair is invariably late-forming; and SO photophores are often the last to form on species possessing this pair.

Larvae and pro-metamorphic specimens of Atlantic material tentatively identified as *Polymetme*, have most of the ventral photophores formed, much in *Ichthyococcus*. Larval stages, up to ca. 16 mm are known for *Woodsia nonsuchae* and *Yarrella argenteola*, but not metamorphosing specimens. For both, metamorphosis is assumed to be similar to *Ichthyococcus*. Developmental stages are unknown for *Triplophos* and *Photichthys*.

The genera of gonostomatids-sternoptychids with a protracted metamorphosis and gradual formation of all body photophores can be broken down into 3 clusters of genera:

1. Genera with all photophores remaining individually separate, but with a protracted metamorphosis: *Gonostoma*, *Bonapartia*, and *Margrethia*.

2. *Maurolicus* and 6 related genera having photophores in clusters with common bases: *Danaphos*, *Valenciennellus*, *Araiophos*, *Argyripnus*, *Sonoda*, *Thorophos*, and *Neophos*.

3. The 3 genera of the family Sternoptychidae: *Sternoptyx*, *Argyropelecus*, and *Polyipnus*.

I will deal first with the group that has the least specialized photophores:

Gonostoma, *Bonapartia*, and *Margrethia*. All 3 genera lack photophores on the isthmus, and the lateral (OA) series of photophores is lacking on *Bonapartia* and *Margrethia*.

Developmental series have been described for 3 species of *Gonostoma*: *G. denudatum* (Sanzo, 1912), *G. elongatum* (Jespersen and Taning, 1919 as sternoptychid larva B; Grey, 1964 as *G. elongatum*) and *G. gracile* (Kawaguchi and Marumo, 1967), and for *Bonapartia pedaliota* (Jespersen and Taning, 1919; Grey, 1964), and *Margrethia obtusirostra* (Jespersen and Taning, 1919; Grey, 1964). I have been fortunate in obtaining larvae and/or metamorphosing specimens of the 3 remaining species of *Gonostoma*: *G. atlanticum*, *G. bathyphilum* and *G. ebelingi*, hence developmental stages are known for all species of this group.

Gonostoma appears to be the pivotal genus with respect to photophore development. Among species of *Gonostoma*, photophores may be formed gradually over a rather extended size range as in *G. elongatum* (Fig. 1B), *G. denudatum*, *G. bathyphilum* (Fig. 1C), and probably *G. ebelingi* (Fig. 1D) - or somewhat more rapidly as in *G. gracilis* and *G. atlanticum* (Fig. 1E). The forms with gradual development are closely allied in development to *Bonapartia* and *Margrethia*, as well as to the Maurolicine and sternoptychid genera. The gradual formation of photophores during a protracted metamorphosis is a major evolutionary trend first evidenced in *Gonostoma.*

The OP_3 pair of photophores is the first to form in all 6 species of *Gonostoma* as well as in *Margrethia* and *Bonapartia.* The next photophores to form (1 or several) are in the PV series, but otherwise the sequence is various, as among the above species (Table 1).

The sequence of photophore formation is contrastingly different in two species of *Gonostoma* with a protracted metamorphosis - *G. denudatum* and *G. elongatum.* In the latter the metamorphosis stage extends from about 6.0 mm to 22.5 mm. Although photophores form gradually in all groups, the sequence among photophore groups is as follows in *G. elongatum*: OP, PV, BR, VAV, ORB and AC, OA and SO. The addition of photophores to the AC group occurs only after most PV and VAV photophores are formed; the initial photophore to form is an inner photophore of the anterior AC group. In contrast, photophores form much later on *G. denudatum* (between ca. 18-34+ mm) and in a different sequence: OP, PV, posterior AC group, BR and VAV, anterior AC group, ORB and OA, SO. Photophores begin forming in the posterior AC group immediately after the first PV photophore is laid down. When photophores are formed in the anterior AC group the 3rd or 4th is laid down first and additional photophores are added both anteriorly and posteriorly.

Metamorphosis in *Margrethia obtusirostra* occurs gradually between about 5.8 to 19.0 mm; photophores are added in the following sequence: OP, PV, VAV and AC (both groups), BR, ORB, and SO. Metamorphosis in *Bonapartia pedaliota* according to Grey (1964) occurs between ca. 9 to 25 mm and is rather similar in sequence to *G. elongatum.*

Although the first few photophores are laid down gradually in *Gonostoma atlanticum,* most of the ventral photophores are laid down as a group. The same general pattern of photophore formation has been described for *Gonostoma gracile* (Kawaguchi and Marumo, 1967). The development of ventral photophores in these two species contrasts sharply with the patterns described above. The lateral series of photophores are laid down after the ventral, much as in *Pollichthys* or *Ichthyococcus.*

Among Maurolicine genera and species rather complete developmental series are known for *Maurolicus mulleri* (Holt and Byrne, 1913; Jespersen and Taning, 1926; Sanzo, 1931; Okiyama, 1971), *Valenciennellus tripunctulatus* (Jespersen and Taning, 1919; Grey, 1964), and *Danaphos oculatus* (original) and less complete series for *Araiophos eastropas* (Ahlstrom and Moser, 1969) and *Argyripnus atlanticus* (Badcock and Merritt, 1972). Information on sequence of photophore formation is contained in Table 2.

The life-history stages are best known for *Maurolicus mulleri* (Fig. 2A) - a fascinating species from egg to adult. Photophores are precociously laid down in this species on larvae as small as 5.5 mm. The first to form are branchiostegal photophores, followed soon by PV photophores. The OP_3 pair form as early as 6.7 mm, the ORB pair soon after (6.9 mm), IP and AC photophores begin to form by 7.5 mm, VAV by 8.6, and OA by 9.0 (see Table 2). Photophore formation is complete by 19.0 mm or sooner. The AC photophores in *Maurolicus* are divided into 3 groups consisting of: an anterior single photophore, a large middle cluster (13-14 photophores), and a posterior cluster (ca. 8 photophores). The first AC photophores to form are in the large middle cluster, but soon thereafter they also form in the posterior cluster. The early forming photophores are in the middle of each cluster and photophores are added in both directions. This pattern appears to be similar to that described for *Margrethia* and *Bonapartia.*

Table 1. Sequence of photophore formation in *Gonostoma*, *Bonapartia*, and *Margrethia*

		ORB	OP	SO	BR	PV	VAV
Gonostoma elongatum	adult	1	3	1	9	15	(4)-5
	6.0	0	1	0	0	0	0
	7.5	0	1	0	0	5	0
	10.2	0	1	0	2/1	10	2
	13.0	0	1	0	2	11	3
	14.0	1	1	0	2	11	2/3
	16.7	1	1	0	3	11	4
	22.5	1	3	1	9	15	5
Gonostoma denudatum	adult	1	3	1	9	15-16	5
	18.25	0	1	0	0	1	0
	19.0	0	1	0	0	2	0
	20.75	0	1	0	1	3	1
	24.75	0	1	0	3	6	3
	29.65	0	2	0	5	14	5
	34.0	1	3	0	9	16	5
	39.0	1	3	1	9	16	5
Gonostoma gracile	adult	1	2	1	9	13-15	4-5
	15.5-17.0	0	1	0	0	0	0
	20.0	1	2	1	2	13	5
	22.0	1	2	1	9	14	4
Gonostoma ebelingi	adult	1	2	1	9	15	10
	13.8	0	1	0	0	7	0
	15.0	0	1	0	0	9	0
Gonostoma bathyphilum	adult	1	2		9	11-12	4-5
	11.0	0	1	0	0	5	0
	14.8	1	1	0	4	10	2
Gonostoma atlanticum	adult	1	2	1	9	15-16	5
	12.0		1				
	13.0	0	1	0	0	1	0
	14.5	0	1	0	0	2	0
	18.8	1	2	0	9	16	5
Margrethia obtusirostra	adult	1	3	0	9-12	13-15	4
	5.8	0	1	0	0	2	0
	6.4	0	1	0	0	6	2
	8.0	0	1	0	2	10	4
	11.3		2	0	6	14	4
	15.0	1	3	0	9	14	4
Bonapartia pedaliota	adult	1	3	1	11-13	14-15	5-(6)
	9.5	0	1	0	2	3	0
	12.0	0	1	0	4	5	2
	14.0	1	1	0	5	10	4
	16.0	1	1	0	6	11	5
	23.0	1	3	0	11	14	5

Table 1. (continued)

AC	OA + ODM	Source
21-23	13-15	Grey 64
0	0	Orig
0	0	Orig
0	0	Orig
0	0	Orig
1+	0	Grey
1+	0	J & T 19
22	13	Grey 64
17-20	13-15	Grey 64
0	0	Sanzo 12
+2	0	Sanzo 12
+3	0	Sanzo 12
3 + 3	0	Sanzo 12
11 + 3	0	Sanzo 12
15 + 5	13	Sanzo 12
15 + 5	13	Sanzo 12
17-19	11-12 + 6-7	K & M 67
0	0	K & M 67
17	0	K & M 67
18	12 + 4	K & M 67
19	21	Grey 64
0	0	Orig
0	0	Orig
20-21	14	Grey 64
0	0	Orig
0	0	Orig
19	13	Grey 64
		Orig
0	0	Orig
0	0	Orig
19	0	Orig
13-14 + 3-4	0	Grey 64
0	0	Orig
1 + 2	0	Orig
1 + 2	0	Orig
5 + 3	0	Orig
11 + 4	0	Orig
16-18 + 2-3	0	Grey 64
0	0	Grey 64
0	0	Grey 64
3 + 1	0	Grey 64
5 + 2	0	J & T 19
14 + 2	0	Grey 64

Table 2. Sequence of photophore formation in *Maurolicus muelleri* and allied maurolicine genera

		ORB	OP	SO	BR	IP	PV	VAV	AC	OA	Source
Maurolicus muelleri	adult	1	3	1	(6)	(6)	(12)	(6)	1 + (13/14) + (8)	(2) + 7	Orig
	5.5	0	0	0	(1/2)	0	0	0	-0-	-0-	Orig
	6.2	0	0	0	(2)	0	(2)	0	-0-	-0-	Orig
	6.5	0	0	0	(2)	0	(4)	0	-0-	-0-	Orig
	6.7	0	1	0	(3)	0	(5)	0	-0-	-0-	Orig
	6.9	1	1	0	(4)	0	(8)	0	-0-	-0-	Orig
	7.5	1	1	0	(4)	1	(9)	0	0 + (2) + 0	-0-	Orig
	8.6	1	2	0	(5)	(3)	(12)	(2)	0 + (3) + (3)	-0-	Orig
	9.0	1	2	0	(5)	(3)	(11)	(2)	0 + (3) + (3)	1	Orig
	9.7	1	3	0	(5)	(5)	(11)	(3)	0 + (4) + (6)	(2) + 1	Orig
	10.8	1	3	0	(6)	(5)	(12)	(4)	0 + (5) + (6)	(2) + 2	Orig
	13.5	1	3	0	(6)	(6)	(12)	(6)	0 + (9) + (7)	(2) + 6	Orig
Danaphos oculatus	adult	1	3	0	(6)	(3) + (4)	(11)	(5)	(3) + 16 + (4) + 1	6	Orig
	16.5	0	0	0	(2)	-0-	0	0	-0-	0	Orig
	16.5	0	0	0	(3)	-0-	(3)	0	-0-	0	Orig
	19.2	0	0	0	(4)	-0-	(10)	0	-0-	0	Orig
	21.0	1	1	0	(5)	(2) + (4)	(10/11)	0	(2) + 0 + 0 + 0	0	Orig
	21.3	1	1	0	(4/5)	(3) + (4)	(10)	0	(3) + 0 + (2) + 0	0	Orig
	21.8	1	2	0	(5)	(3) + (4)	(11)	(2)	(3) + 8 + (4) + 0	2	Orig
	24.2	1	2	0	(6)	(3) + (4)	(11)	(2)	(3) + 9 + (4) + 0	2	Orig
Valenciennellus tripunculatus	adult	1	3	0	(6)	(3) + (4)	(16-17)	(4-5)	(3) + (3) + (3) + (2) + (4)	(2) + 3	Grey 64
	8.6	0	0	0	(3)	-0-	(3)	0	-0-	-0-	Orig
	9.5	0	0	0	(4)	-0-	(6)	0	-0-	-0-	Orig
	12.0	0	0	0	(4)	-0-	(13)	(2)	-0-	-0-	Orig
	13.2	0	0	0	(4)	-0-	(14)	(3)	-0-	-0-	Orig
	17.0	1	2	0	(4-5)	(3) + (4)	(15)	(5)	(3) + (3) + 0 + (3) + (4)	(2)	Grey 64
Araiophas eastropas	adult	1	1	0	(6)	(2)	(3) + 3-4 + (2)	(3)	(2) + 2 + (2)	no	A & M 69
	11.2	0	0	0	(3)	0	(2)	0	-0-	-	A & M 69

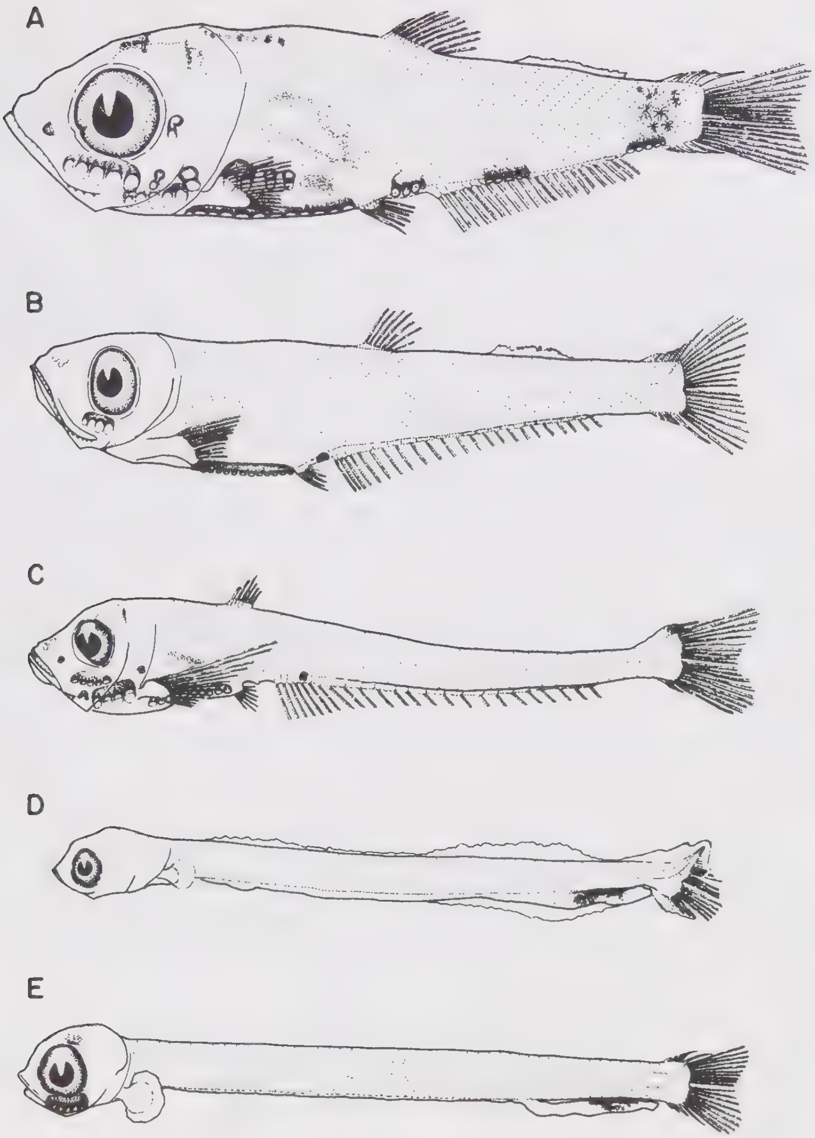

Fig. 2. Larvae and metamorphosing specimens of gonostomatids. (A) *Maurolicus muelleri*, 10.8 mm, middle metamorphosis. (B) *Valenciennellus tripunctalatus*, middle metamorphosis. (C) *Danaphos oculatus*, middle metamorphosis. (D) Maurolicine alpha - 7.5 mm larvae. (E) Same, 16.0 mm, early metamorphosis

The initiation of photophore formation on *Valenciennellus tripunctulatus* is not quite as precocious as in *Maurolicus*: BR and PV photophores were first observed on 8.6 mm larvae. The sequence also is different: the VAV photophores form relatively much sooner and the AC group much later (Fig. 2B). These differences in sequence facilitate identification.

Larvae of *Danaphos* and *Valenciennellus* occur together in the eastern Pacific, and small specimens are somewhat similar in appearance. *Danaphos* has a shorter gut; both lack pigmentation (except peritoneal). Hence it is fortunate that *Valenciennellus* begins photophore formation at a relatively small size, whereas *Danaphos* delays photophore formation until about 16.5 mm. As in the preceding 2 genera, photophore formation begins in the BR and PV groups. Thereafter the sequence differs from that in *Maurolicus* and *Valenciennellus*, although it is closer to *Maurolicus* (Fig. 2C).

We have observed only larvae and early transformation-stage specimens of *Araiophos eastropas*. The larvae have a substantially longer gut than the preceding 3 genera (snout-anus in *Araiophos* larvae - 72-79% SL). Metamorphosis beings at about 11.0 mm, with the initial formation of photophores in the BR and PV groups.

The developmental pattern, shared in common by all Maurolicine genera for which metamorphic stages are known, is a gradual metamorphosis with the initial formation of photophores in the BR and PV groups.

I am illustrating two sizes of a fascinating Maurolicine larvae that I call simply "alpha" (Fig. 2D, E). The eye is large, to the point of dominating the head; the gut is exceptionally long for a gonostomatid larva (ca. 95% SL). The posterior portion of the gut is becoming detached from the body in the larger specimen, undoubtedly to accommodate the anal fin which hasn't yet begun to develop. However, the branchiostegal photophore group is complete - a cluster of 6 branchiostegal photophores with a common base. No other photophores have formed. The number of myomeres is in the mid-40's. The larva is obviously of a primitive Maurolicine gonostomatid. Among described species only *Neophos nexilis* Myers has this number of vertebrae (44-45, S. Weitzman, pers. comm.). If not this, it represents an undescribed form.

Inasmuch as the Maurolicine genera are as closely related to the Sternoptychidae as to the gonostomatid with separate photophores, I will give a little information on the sequence of photophore formation in *Sternoptyx diaphana* and *Argyropelecus lychnus*.

The first photophore pair to form in *Sternoptyx* is the subopercular pair (OP_3). This is soon followed by BR, and then both PV and IP photophores. The lateral (suprapectoral) photophores begin forming before the AC photophores. Marked changes occur in body depth and form during transformation which occurs over a relatively short size range, as measured by SL.

I have not been as successful with transforming specimens of *Argyropelecus lychnus* in tracing the sequence in which photophores form. When I have found transforming specimens, a number of photophores were already developed. The BR and IP groups form their full complement of photophores before the PV group and the AC photophores begin to form before the VAV group.

In my attempt to coordinate what is known concerning metamorphic patterns, I have separated the gonostomatids-sternoptychids into 4 groups of genera.

Group A. Genera in which most or all ventral photophores are laid down initially during a pro-metamorphic (white photophore) stage and which have all photophores separate - *Vinciguerria, Cyclothone, Ichthyococcus, Pollichthys, Diplophos*, and presumably *Woodsia, Yarrella*, and *Polymetme.*

Group B. Genera with a gradual, protracted metamorphosis, with all photophores remaining individually separate and initial photophore formation in OP and PV groups - *Gonostoma, Bonapartia*, and *Margrethia.*

Group C. Genera having some or most photophores in clusters with common bases, a gradual, protracted metamorphosis, with initial photophore formation in BR and PV groups - *Maurolicus, Valenciennellus, Danaphos, Araiophos, Argyripnus*, and presumably *Thorophos, Neophos*, and *Sonoda.*

Group D. More highly specialized fishes having most photophores in clusters with common bases; they have a gradual, protracted metamorphosis with striking changes in body form - sternoptychid genera *Sternoptyx, Argyropelecus*, and *Polyipnus.*

The triad of genera in group B is a closely knit assemblage, with *Gonostoma* the pivotal genus. Metamorphosis among the 6 species of *Gonostoma* shows much greater diversity than among species of other genera, as for example *Vinciguerria* or *Cyclothone.* As pointed out earlier, all species of *Gonostoma* first form the OP_3 pair and 1 to several PV pairs before forming other photophores; thereafter the patterns diverge. Most of the photophores of the ventral series are laid down fairly rapidly in *G. gracile* and *G. atlanticum* - features that ally this pair of species to the genera included in group A. The species of *Gonostoma* with a protracted metamorphosis, as for example *G. elongatum* and *G. denudatum*, share developmental features with the Maurolicine genera (group C).

Certain developmental patterns are common to all 4 groups, and to me the most striking of these is the pattern of photophore formation within the AC group. During formation of these photophores there is usually a sharp separation into 2 groups - a posterior group of 2 or more AC photophores separate from the main AC group. In the anterior AC group, 1 or several of the inner photophores develop initially and are added to both anteriorly and posteriorly. When the posterior group contains 3 or more photophores, they form similarly; eventually the 2 groups may unite. This pattern of AC development is found in *Pollichthys, Ichthyococcus*, and *Diplophos* in group A, in several species of *Gonostoma* (example *G. denudatum*), as well as *Bonapartia* and *Margrethia* in group B, and in a modified form among Maurolicine (group C) and Sternoptychidae (group D) genera, i.e. separation in 3 or more AC groups, each with an inner to outer sequence of photophore formation.

Although *Gonostoma* is considered the pivotal genus, with developmental patterns that show relationships to both the Maurolicine line and the genera in group A; I consider it closer to the genera in group A. There are objections to considering it as basic stock from which the other lines could be derived.

First of all there is the problem of isthmal photophores; these are lacking in *Gonostoma-Margrethia-Bonapartia* but developed in all Maurolicine genera, and in all genera of group A except *Cyclothone.* It is more logical to derive both lines from an ancestor that possessed this group of photophores than from one that lacked it. There is the additional problem of separate photophores vs. clustered photophores when relationships with Maurolicine genera are considered. We are also confronted with the fact that in some larval characteristics, such as gut length, several Maurolicine genera appear to be more primitive than *Gonostoma*. Undoubtedly the divergence between species with single vs. clustered photophores came early in the evolution of gonostomatid-like fishes.

Bassot (1966, 1970) used the structure of light organs to trace evolutionary lineages among stomiatoid fishes. He described 3 types of light organs, the most primitive type was found in *Gonostoma, Bonapartia, Cyclothone*, and *Diplophos (Manducus)*; a distinctively different type in Maurolicine and sternoptychid genera; and third type in *Vinciguerria, Ichthyococcus, Yarrella* and in most stomiatoids (*Chauliodus, Stomias*, etc.). His findings based on light organs are in general agreement with the groups discussed above, except for placement of 2 genera - *Cyclothone* and *Diplophos*.

The question arises as to the relation of the Maurolicine genera to the three genera of sternoptychids. The latter show more marked specializations in both larval and adult characters: they are a more specialized group than the Maurolicine genera. The two assemblages have several important characters in common: clustered photophores, a protracted metamorphic stage, and similar structure of light organs. The Maurolicine genera certainly are as closely related to the sternoptychids as to other genera of gonostomatids. The present separation of the two groups into separate families is artificial. If the sternoptychids are combined with the gonostomatids, the former would have priority as the family name. I personally favor the inclusion of all gonostomatid-sternoptychid fishes in a single family. If divisions are to be made within the family, the genera with clustered photophores would constitute one subfamily, those with separate photophores the other. I find the genus *Gonostoma* too ambivalent in developmental patterns to separate it sharply from other gonostomatid genera with separate photophores.

SUMMARY

The gonostomatid light fishes rank second only to myctophid lantern fishes in abundance in the sea. The family is made up of 20 genera and approximately 60 species, all possessing photophores. Photophore patterns have been used as a primary character in adult taxonomy. The diversity of patterns of photophore acquisition - ranging from most photophores being formed simultaneously to a gradual formation of photophores during a protracted metamorphosis - is used to trace relationships among gonostomatid genera. On the basis of metamorphic patterns, the gonostomatid genera fall into three groups. One group includes genera in which most or all ventral photophores are laid down initially during a "white" photophore stage and which have all photophores individually separate (*Vinciguerria, Cyclothone, Ichthyococcus*, etc.). The second group includes genera with a gradual, protracted metamorphosis, but with all photophores individually separate (*Gonostoma, Bonapartia,* and *Margrethia*). The third group includes genera having some or most photophores in clusters with common bases which are laid down gradually during a protracted metamorphosis (*Maurolicus, Valenciennellus, Danaphos, Araiophos*, etc.). *Gonostoma* is considered the pivotal genus with developmental patterns that show relationships to the other two groups. It is pointed out that the third group is as closely related in developmental pattern to the sternoptychids as to other genera of gonostomatids, and that the two families should be combined into a single family.

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Chaetognatha

The phylum Chaetognatha comprises a group of small wormlike marine animals with transparent to translucid or opaque arrowshaped bodies, hence their common name arrowworms. The phylum consists of about seven extant genera and one fossil genus. There are more than 50 species, most of which are in the genus *Sagitta*. The size of the Chaetognatha ranges from about three millimetres to more than 100 millimetres; species inhabiting colder waters generally are larger than those from tropical seas. Chaetognatha are hermaphroditic (having both male and female sex organs, or gonads). The body is divided into head, trunk, and tail by two transverse walls or membranes and has lateral fins and a tail fin. Respiratory, circulatory, and excretory systems are not properly developed.

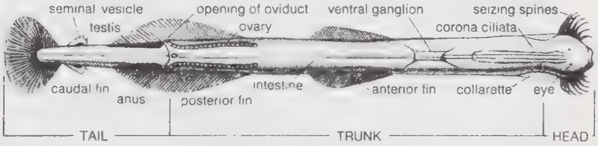
Size and distribution

Natural history. *Life cycle.* Chaetognaths are protandric (*i.e.*, male gonads mature earlier than female gonads). Most chaetognaths die after spawning, although some undergo cycles of maturity and often also growth. Cross-fertilization has been observed, the sperm passing from the storage organs called seminal vesicles, which open out to the exterior, to the seminal receptacle (tube along the female gonads) of another individual. The eggs are fertilized by the sperm either shortly before or as they are laid, in a part of the duct common to the oviduct and to the seminal receptacle. In several genera (*e.g.*, *Eukrohnia*, and probably also in the genera *Bathyspadella*, *Krohnitta*, and *Heterokrohnia*), mature eggs and larvae are enclosed in a sac formed at the opening of oviducts. In *Pterosagitta*, eggs are laid in a capsule; in *Sagitta*, eggs are discharged into the surrounding water one at a time in several cycles; and in *Spadella*, eggs have an adhesive coat and a stalk and attach to any surface.

Ecology. Chaetognaths are voracious feeders; they consume copepods, euphausiids, fish larvae, medusae, other chaetognaths, cladocerans, amphipods, appendicularias, and eggs and larvae of various animals. Chaetognaths inhabit oceans, seas, and coastal lagoons. Although some species are cosmopolitan, others are restricted to a geographical region or an ocean. Southeast Asia seas have the largest number of species. Epiplanktonic species—*i.e.*, those within 200 metres of the water surface—increase in numbers from the poles to the Equator. Mature chaetognaths inhabit deeper oceanic layers than do the young.

Few chaetognaths have parasites; those that do are more often parasitized in neritic (close to shore) waters than in the open ocean.

Form and function. The body of a Chaetognatha is covered by a cuticle of cells (called collarette when thickened). The head has hooks (curved, grasping spines) covered by a hood or thin fold of skin, which retracts when the arrowworm is catching prey. Head muscles control the movement of hooks, teeth, and mouth; body muscles are longitudinal with some transverse bands. Chaetognaths swim with dartlike movements by contracting the longitudinal muscles and flapping the tail.



Body plan of arrowworm (*Sagitta bipunctata*).

The nervous system consists of a large cerebral ganglion with sensory nerves (*e.g.*, optic, coronal). The cerebral ganglion is connected with the ventral ganglion by a pair of nerve cords. Additional ganglia and nerves spread along the body. Touch receptors, small, round, ciliated (hairlike) prominences, are scattered over the body.

There is evidence that regeneration of the head and the anterior part of the body occurs; during regeneration, the eyes appear first, then the mouth and hooks. The eyes contain a pigmented central cell, which encloses five clusters of photoreceptor cell processes (or ocelli). A conical body found in the photoreceptor cell either may guide the animal as it swims or act as a resonator. The pigmented central cell may have various shapes (*e.g.*, starlike) in different species. No pigment is present in most deep-sea dwelling species.

The corona ciliata

The corona ciliata is an olfactory (smell) receptor or chemoreceptor peculiar to the Chaetognatha and is formed by a series of rows of ciliated cells forming a ring or elongated oval at the neck or extending toward the head and the trunk. The digestive tract, which is lined by glandular and absorptive cells, extends from the mouth to the anus and is supported by a mesentery. The central mesentery divides the trunk and tail into two cavities. Trunk and tail regions are filled with a colourless fluid that circulates forward along the body walls and backward in the medial region of the body. Two ovaries, filled with rows of unfertilized eggs, extend along the trunk and are attached to the sides of the body by a mesentery. The seminal receptacle in the oviducts stores sperm after copulation. The testes are located in the tail cavities; a spermduct, or vas deferens, connects the testes with the seminal vesicles, which open out from the body. The ovaries in the trunk, therefore, are isolated from the testes in the tail, with no internal communication between male and female gonads. The seminal vesicles burst when filled with sperm, ejecting the spermatozoa into the surrounding waters or into the seminal receptacle of another individual.

Relationships and classification. The Chaetognatha is an isolated phylum in the animal kingdom; *i.e.*, comparative anatomy and embryology fail to link these animals with any other group. Chaetognaths have been considered as worms, and attempts have been made to relate them to many animal groups (*e.g.*, Heteropoda, Annelida, Nematoda, Arthropoda). They also have been placed taxonomically between Annelida and Nematoda. Structure of the chaetognath eye, however, indicates a probable evolutionary relationship to echinoderms and chordates.

The highest taxonomic rank in the phylum Chaetognatha is the genus. Genera are distinguished by the number, position, and extension of lateral fins and by the teeth. The presence of two pairs of lateral fins separates *Sagitta* from the other genera. Species within each genus are identified by minor differences (*e.g.*, shape and position of anatomical structures). There are at least six other genera of chaetognaths: *Spadella, Eukrohnia, Krohnitta, Heterokrohnia, Bathyspadella*, and *Pterosagitta*. A mid-Cambrian fossil species *Amiskwia sagittiformis* is also known.

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DISTRIBUTION OF SIPHONOPHORES IN THE REGIONS ADJACENT TO THE SUEZ AND PANAMA CANALS

Angeles Alvariño[1]

ABSTRACT

These studies are based on the material collected by Israeli cruises in the eastern Mediterranean and the Red Sea (Gulf of Elat), and by Scripps Institution of Oceanography Expeditions in the Caribbean and the Pacific regions adjacent to the Panama Canal. Published information on the distribution of siphonophores in those areas and in adjacent regions is included. Distributional tables and maps are also included.

The eastern Mediterranean collections encompass 21 species of siphonophores. Most of these species have been previously recorded in the western Mediterranean. *Eudoxia russelli* (eudoxid of *Chelophyes appendiculata*), *Sulculeolaria angusta*, and *S. chuni* have not been previously observed in any Mediterranean region. New records for the eastern Mediterrranean are: *Ch. contorta, Diphyes bojani, D. dispar, Lensia campanella, L. meteori, L. subtilis, S. quadrivalvis, S. turgida, Rosacea plicata, Physophora hydrostatica*, and *Apolemia uvaria*. Few species previously observed in the Mediterranean were not present in the collections here analyzed.

Fifteen species of siphonophores appeared in the material from the Gulf of Elat. New records for the Red Sea are *Ch. appendiculata, E. russelli, Diphyopsis mitra*. The other species present (*Ch. contorta, Diphyes dispar, L. subtilis, S. chuni, S. quadrivalvis, Abylopsis eschscholtzi, A. tetragona, Enneagonum hyalinum, Cordagalma cordiformis, Agalma elegans,* and *A. okeni*) have been previously observed in the Red Sea.

New records at both sides of the Suez Canal which could be considered indicative of migration along this waterway are: *Ch. appendiculata* (Mediterranean to the Red Sea), and *S. chuni* (Red Sea to the Mediterranean). However, the species are cosmopolitan in distribution, and the source of the populations in the regions adjacent to the Suez Canal may be in the adjacent oceanic regions.

Thirty species of siphonophores were observed in the Caribbean and Pacific regions adjacent to the Panama Canal. Most of the species are new records for those regions. Twenty one more species, not present in the collections here analyzed, had been previously recorded at either or in both the Caribbean, Gulf of Mexico and/or in regions of the Pacific adjacent to the area surveyed.

Particular attention is devoted to the distribution of closely related pairs of allopatric species, *Muggiaea atlantica–M. kochi*, and *Ch. appendiculata–Ch. contorta. Muggiaea kochi* (neritic species) and *Ch. appendiculata* inhabit the Caribbean, Gulf of Mexico and adjacent regions of the western tropical Atlantic. *Muggiaea atlantica* (neritic species) and *Ch. contorta* inhabit the Pacific regions off Mexico and Central America. However, few specimens of *Ch. contorta* and *M. atlantica* were also observed in the Caribbean at locations near the opening of the Panama Canal, and specimens of *Ch. appendiculata* and *M. kochi* occurred at locations in the Pacific close to the Panama Canal. This distributional incidence may suggest that migration or artificial transport is taking place via the Panama Canal. It is also indicated that few specimens of *L. challengeri* (Indo-Pacific species) were observed near the opening of the Panama Canal in the Caribbean.

New data have been published on the siphonophores of the regions adjacent to the Suez Canal (eastern Mediterranean and the Red Sea), as well as for the regions adjacent to the Panama Canal (western Caribbean and the Central American Pacific). Bigelow and Sears (1937) included data on the distribution of the siphonophores in the eastern Mediterranean, and Lakkis (1971) on the Lebanese region. Schneider (1898), Totton (1954), and Halim (1969) presented information on the siphonophores of the Red Sea. Bigelow (1911) analyzed the siphonophores of the eastern tropical Pacific, which included few locations in the regions here surveyed; Alvariño (1968, 1972) studied the siphonophores of the tropico-equatorial oceanic regions, and Alvariño (1971) covered the Central American Pacific including also a compilation of distributional data for the world oceans.

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The present work constitutes a more detailed survey on the siphonophores of the regions adjacent to the above mentioned interoceanic canals. These studies are based on the Siphonophorae material (65 plankton samples) collected by Israel in the eastern Mediterranean during 1967, 1968, 1969, and 18 plankton samples (Red Sea, 1969, 1970) corresponding to two locations in the Gulf of Elat; and the 64 plankton samples from Scripps Institution of Oceanography Expeditions (La Creuse 1962, Bonacca 1963, *Thomas Washington* 1969) in the Caribbean and Pacific regions adjacent to the Panama Canal. The Scripps Institution collections covered larger regions than the area in which the present studies are concentrated, and the total collections of the mentioned expeditions have been analyzed and the results included in Alvariño (1968, 1971, 1972).

The present studies chiefly concern with the distribution and some ecological aspects of the siphonophores. The subject is treated under two parts: 1) distribution of siphonophores in the eastern Mediterranean and the Red Sea, and 2) the siphonophores of the western part of the Caribbean and the Central American Pacific.

The pattern of distribution of the species is presented. Tables with the distribution of the species include also references on previous records for the regions.

Maximum density for most of the species off Israel and around Cyprus can be attributed to the high productivity of the region (Lakkis, 1971).

The present study also indicates the Red Sea includes fewer species than the Indian Ocean. This factor may be related to the high salinity and temperature of the Red Sea, as well as to the shallowness of the sill at Bab el Mandeb.

The incidence of both polygastric and eudoxid forms in most of the samples shows breeding is taking place in those regions, and that reproduction may be an uninterrupted process along the year.

A large number of species of siphonophores are truly cosmopolitan, inhabiting the Arctic, Antarctic, Indian, Pacific, and Atlantic Oceans, whereas other species inhabit only the Atlantic, Pacific, and Indian Oceans (Alvariño, 1971), and some others are restricted to the Indian Ocean, adjacent waters and the southeastern Asiatic regions, while few are restricted to either the Atlantic or the Indo-Pacific regions.

Owing to the above mentioned biogeographic considerations, particular emphasis in the distribution of the species should be dedicated to the pairs of closely related species allopatric in distribution. The pairs to be considered correspond to the Panamanian region: *Chelophyes appendiculata–Ch. contorta* (respectively related to cold-temperate, and warm waters), *Muggiaea atlantica–M. kochi* (inhabiting respectively the neritic temperate and neritic warm waters), and *Lensia challengeri–L. fowleri* (respectively Indo-Pacific and Atlantic species).

The evidence of a two way migration "via" the Panama Canal, as shown by the distribution presented by several species at the regions adjacent to the entrance to the Panama Canal, could be active, by progression of the population along the waterway, or passively transported in the ballast waters or the waters used in the cooling system of ships. Therefore, migrations could be also greatly intensified or enhanced by passive transport along the canal.

METHODS

The plankton samples here analyzed were not collected in uniform manner. The plankton collections from the eastern Mediterranean and the Gulf of Elat were obtained with a standard plankton net of the Villefranche type, as designed and described by Working Party No. 2 (1968). The net has a mouth internal diameter of 57 cm, a total length of 261 cm, and 200-μ mesh. Vertical, oblique, and horizontal tows were taken. The vertical and oblique hauls in the eastern Mediterranean and the Gulf of Elat reached from 200 m to the surface, and the horizontal tows were obtained at various depths in the upper 200 m at a speed of 2-3 knots during 10 min.

The material from the Scripps Institution collections corresponds to 1–m net oblique hauls taken from about 140 m to the surface, and at less than 100 m or less than 50 m in shallow waters; and the ½–m net oblique tows were obtained from about 150 m to the surface and the horizontal hauls at various depths between 50 and 0 m.

Each total plankton sample was analyzed for siphonophores, and the number of specimens determined for both polygastric and eudoxid forms. However, owing to the diversity of the collecting methods used, and the time span covered by the collections, quantitative data are not considered, and only qualitative data are included in the presentation of the results.

DISTRIBUTION OF SIPHONOPHORES IN THE EASTERN MEDITERRANEAN AND THE RED SEA

Twenty-one species of siphonophores were observed in the eastern Mediterranean collections, and fifteen species in the Gulf of Elat (Red Sea) collections.

Eudoxia russelli (eudoxid of *Ch. appendiculata*), *Sulculeolaria angusta*, and *S. chuni* are new records for the Mediterranean.

Chelophyes contorta, Diphyes bojani, D. dispar, Lensia campanella, L. meteori, L. subtilis, Sulculeolaria quadrivalvis, S. turgida, Rosacea plicata, and *Apolemia uvaria* are first records for the eastern Mediterranean. These species have been previously observed in the western Mediterranean. The only previous records of *Ch. contorta* for the Mediterranean correspond to the Alborán Sea (Alvariño, 1957). Therefore, the presence of the species in the Levant Mediterranean basin could be considered a tracer of Atlantic waters. All the Mediterranean species are also found in the Atlantic. Some of the species have permanently established populations in the Mediterranean, while others may be only remains of the Atlantic flow.

Most of the species previously found in the eastern Mediterranean (Bigelow and Sears, 1937; Lakkis, 1971) were also observed in the collections here analyzed.

Some species previously found in the western Mediterranean (*M. atlantica, L. fowleri, Clausophyes ovata, Ceratocymba sagittata, Vogtia pentacantha, V. spinosa, Praya cymbiformis, Amphicaryon acaule, Anthophysa rosea, Rhizophysa filiformis, Cordagalma cordiformis, Athoribya rosacea,* and *Nanomia cara*) have not been observed in the eastern Mediterranean (Alvariño, 1971; Lakkis, 1971) (Table 1).

The most abundant species in both distributional coverage of the surveyed region and in number of species, *Ch. appendiculata, D. dispar, Hippopodius hippopus, Bassia bassensis* were found along the years, and in December appeared scattered or absent (Figures 1, 2, 6, 8). *Eudoxoides spiralis, S. turgida, S. quadrivalvis*, and *S. angusta* followed in decreasing order of abundance in both space covered and number of individuals (Figures 3, 5). These species appeared abundantly off Israel, Lebanon, Syria and around Cyprus. *Sulculeolaria angusta* and *S. turgida* were also found in the Cretan region.

Species with few scattered records are, *E. russelli* (north of Cyprus), *Ch. contorta* (off Israel and between Syria and Cyprus), *D. bojani, M. kochi, L. campanella, L. multicristata, L. subtilis, S. chuni, A. tetragona, R. plicata, A. uvaria, Agalma elegans*, and *Physophora hydrostatica* (spread along the Levant basin). (Figures 1-8.)

It is worthy of notice that the maximum density for most of the species of siphonophores appeared at the easternmost part of the Mediterranean Sea, off Israel and around Cyprus, which can be attributed to the high productivity of the region (Lakkis, 1971).

The species scattered along the eastern Mediterranean, not previously observed in this sea, could be considered tracers of Atlantic waters (Oren, 1971).

The presence of *L. multicristata* (a mesoplanktonic species) off Tira, Israel, could be an indicator of upwelling.

It is well established that the fauna of the eastern Mediterranean is an impoverished fauna from that of the western basin. Many species do not reach the Levant Mediterranean basin, and only appear accidentally there, and few become established in the area. Por (1971) considered that "The colder areas of the Aegean Sea probably constitute an environment in which the Atlantic fauna is much better represented and better fitted to withstand the competition of the tropic immigrants."

Siphonophorae fauna of the Red Sea is poorer than that of the Indian Ocean, both in number of species and in the density of the respective populations. The Gulf of Elat may also include fewer species than the main Red Sea basin. The Gulf of Elat collections correspond to the winter months. Some of the species observed in the Gulf of Elat constitute new records for the Red Sea (*Ch. appendiculata, E. russelli,* and *Diphyopsis mitra*). Por (1971) stated that siphonophores and other holoplanktonic groups have not been found in the Suez Canal waters.

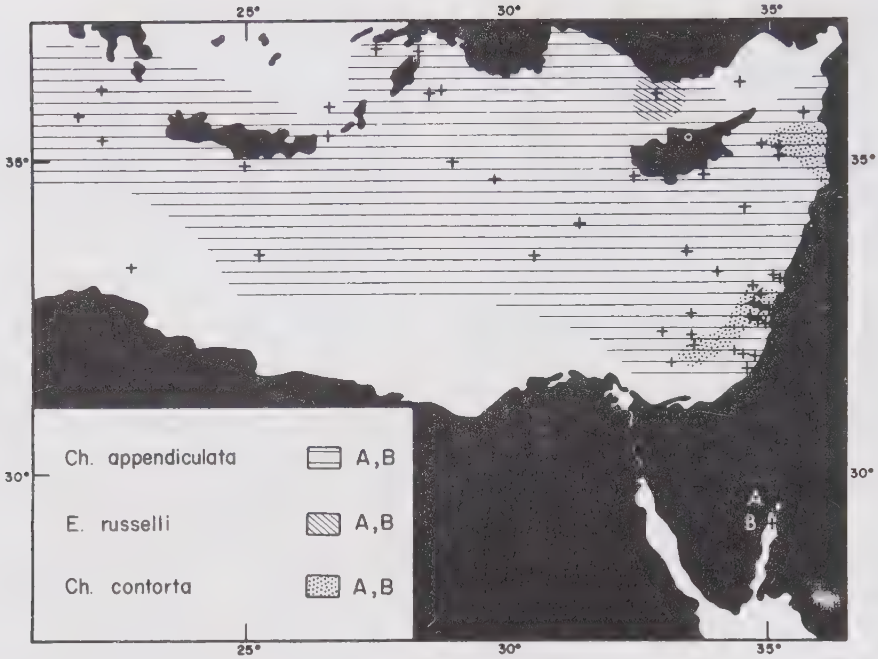
25°
30°
35°
35°
30°
Ch. appendiculata
A,B
E. russelli
A,B
Ch. contorta
A,B
A
B
A

FIGURE 1.—Distribution of *Chelophyes appendiculata*, *Eudoxia russelli*, and *Chelophyes contorta* in the regions adjacent to the Suez Canal.

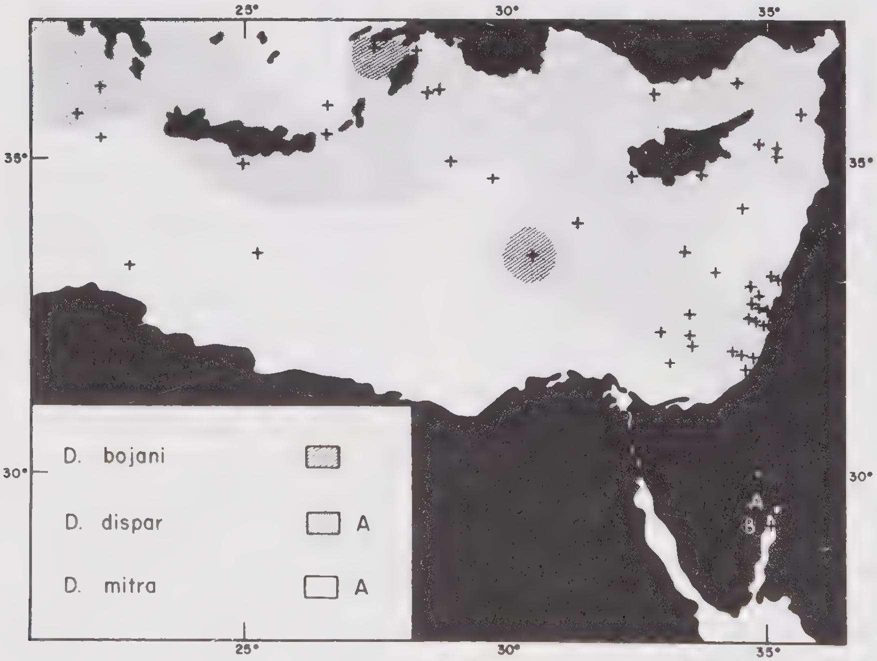
25°
30°
35°
35°
30°
D. bojani
D. dispar
A
D. mitra
A
A
B
A

FIGURE 2.—Distribution of *Diphyes bojani*, *Diphyes dispar*, and *Diphyopsis mitra* in the regions adjacent to the Suez Canal.

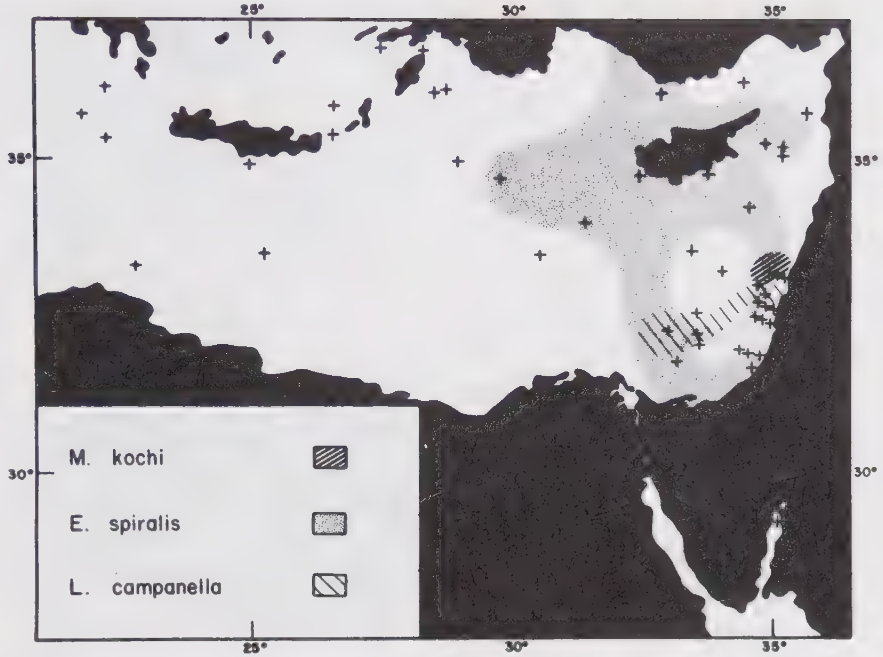
25°
30°
35°
35°
30°
M. kochi
E. spiralis
L. campanella

FIGURE 3.—Distribution of *Muggiaea kochi*, *Eudoxoides spiralis*, and *Lensia campanella* in the regions adjacent to the Suez Canal.

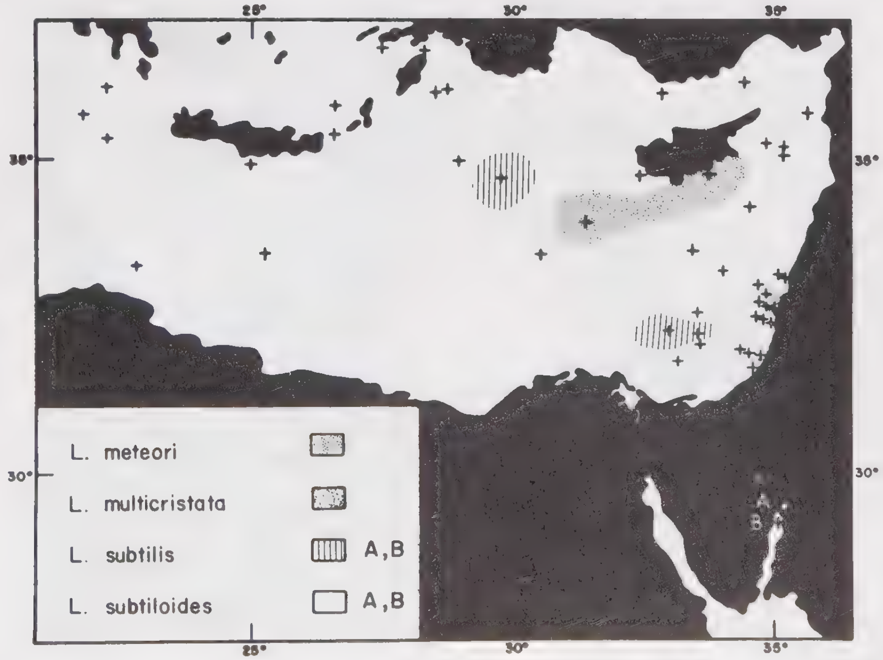
25°
30°
35°
35°
30°
A
B
L. meteori
L. multicristata
L. subtilis A,B
L. subtiloides A,B

FIGURE 4.—Distribution of *Lensia meteori*, *Lensia multicristata*, *Lensia subtilis*, and *Lensia subtiloides* in the regions adjacent to the Suez Canal.

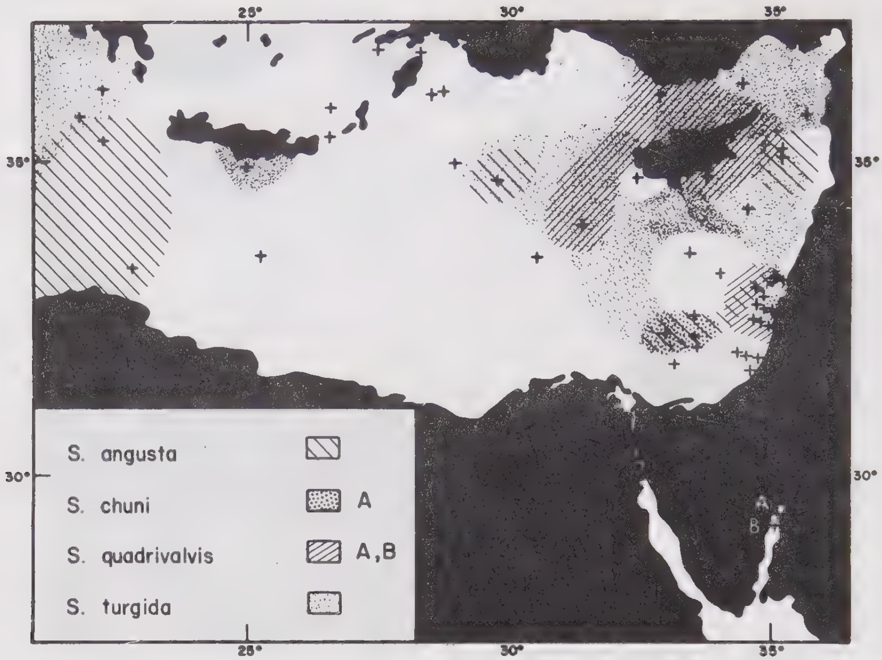
25°
30°
35°
35°
35°
30°
30°
S. angusta
S. chuni A
S. quadrivalvis A,B
S. turgida
A
B
25°
30°
35°

FIGURE 5.—Distribution of *Sulculeolaria angusta, Sulculeolaria chuni, Sulculeolaria quadrivalvis,* and *Sulculeolaria turgida* in the regions adjacent to the Suez Canal.

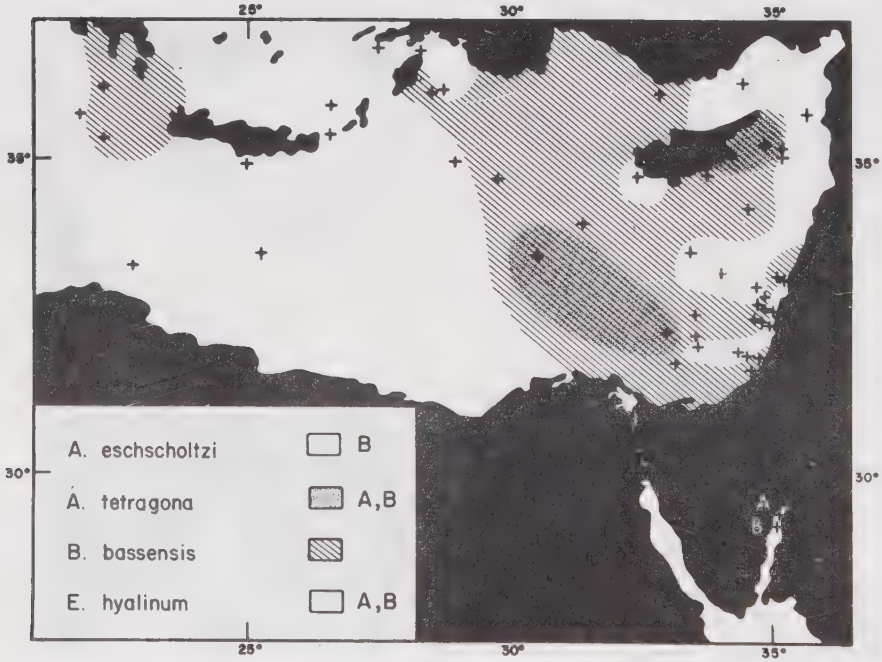
25°
30°
35°
35°
35°
30°
30°
A. eschscholtzi B
A. tetragona A,B
B. bassensis
E. hyalinum A,B
A
B
25°
30°
35°

FIGURE 6.—Distribution of *Abylopsis eschscholtzi, Abylopsis tetragona, Bassia bassensis,* and *Enneagonum hyalinum* in the regions adjacent to the Suez Canal.

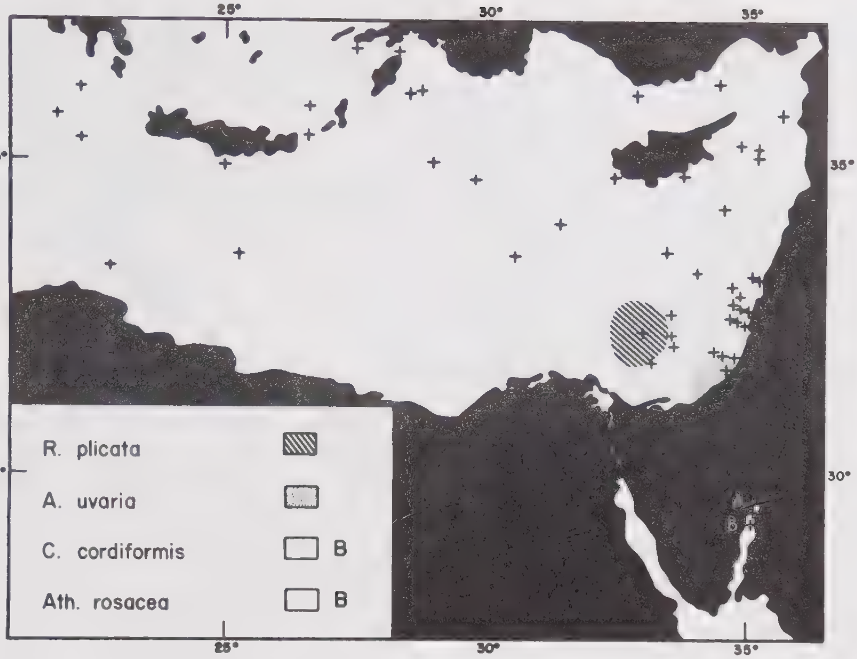
25°
30°
35°
35°
35°
30°
30°
R. plicata ▨
A. uvaria
C. cordiformis ☐ B
Ath. rosacea ☐ B
B
25°
30°
35°

FIGURE 7.—Distribution of *Rosacea plicata, Apolemia uvaria, Cordagalma cordiformis*, and *Athoribya rosacea* in the regions adjacent to the Suez Canal.

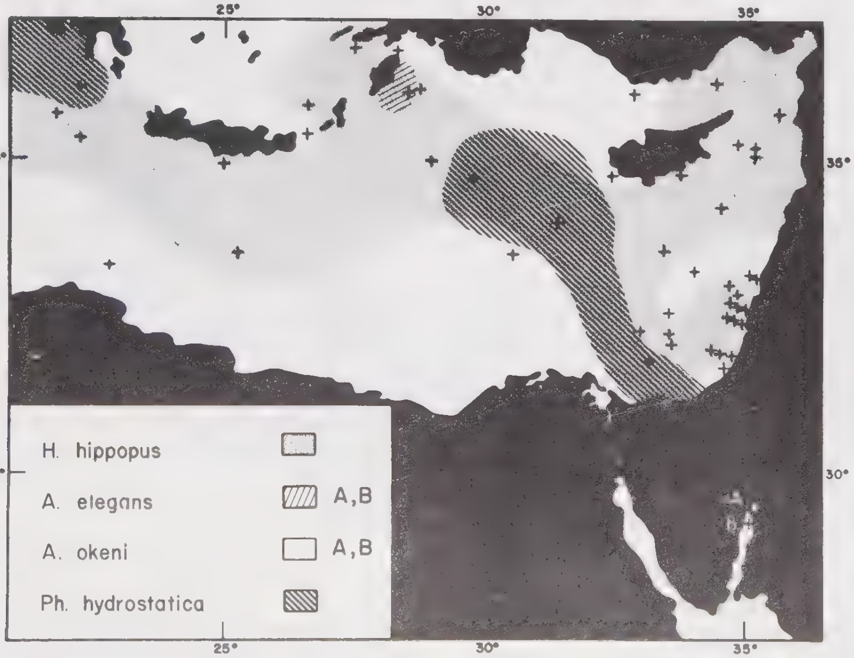
25°
30°
35°
35°
35°
30°
30°
H. hippopus
A. elegans ▨ A,B
A. okeni ☐ A,B
Ph. hydrostatica ▨
B
25°
30°
35°

FIGURE 8.—Distribution of *Hippopodius hippopus, Agalma elegans, Agalma okeni*, and *Physophora hydrostatica* in the regions adjacent to the Suez Canal.

Other new records for the Gulf of Elat are *Diphyes dispar, L. subtilis, L. subtiloides, S. chuni, S. quadrivalvis, A. eschscholtzi, A. tetragona, E. hyalinum, C. cordiformis, A. rosacea, A. elegans*, and *A. okeni*. These species, except *Ch. contorta*, were only previously observed in either the central and the southern Red Sea or both (Figures 1, 2, 4-8). *Ch. contorta* was previously observed in the Gulf of Elat (Furnestin, 1958).

The depth of the sill at Bab el Mandeb does not exceed 100 m (Halim, 1969) and consequently meso and bathypelagic species are extensively excluded from the Red Sea. Halim considered the scarcity of species in the Red Sea as due to the "excluding action of the deep outflow over the sill at the southern entrance of the Red Sea on the deep water species; and . . . the effect of the high (21.5°–22°C) minimum temperature of the Red Sea deep water in inhibiting many species. . . ." He also considers excluding features the "high salinity (40.5–41.0‰) and the very low oxygen content (below 1 ml/l in summer and 2 ml/l at the end of the winter) below sill depth."

Similar interpretation could be applied for the paucity of the Mediterranean siphonophores as compared with the Atlantic, because of the sill at Gibraltar.

Thorson (1971) stated that "the physical-chemical conditions for the animals to pass the Canal have improved enormously although there are still obstacles for the migration of many species."

Seasonal variations in occurrence, abundance and in the distributional pattern presented by the species of siphonophores in both the Levant Mediterranean basin and the Gulf of Elat are to be expected. The various populations may show changes in both location and time of year. These changes may be due to the characteristics of the flow through the Strait of Gibraltar, and Bab el Mandeb respectively, and the characteristics of the circulation in the Mediterranean and the Arabian Sea, as well as the aspects of the vertical migration (Halim, 1969), and the ontogeny of the population.

Most of the siphonophores, except for a few species as explained above, present a wide almost cosmopolitan distribution (Alvariño, 1971). However, species abundant in the western Mediterranean and the Atlantic reaching the easternmost Mediterranean region could be considered "indicators" or tracers of the Atlantic waters. This could be similarly applied to some Indo-Pacific or Indian Ocean species reaching the Red Sea.

SIPHONOPHORES OF THE WESTERN CARIBBEAN AND THE CENTRAL AMERICAN PACIFIC

The pairs of closely related species allopatric in distribution, *Ch. appendiculata-Ch. contorta, M. atlantica-M. kochi*, and *L. challengeri–L. fowleri* deserve special attention.

Chelophyes appendiculata inhabits the temperate oceanic regions, and appears scattered along the tropico-equatorial realm, while *Ch. contorta* presents a distribution restricted to the tropico-equatorial regions (Alvariño, 1971).

Muggiaea atlantica inhabits the neritic temperate eastern Pacific, Transition region (band between the Subarctic and Central Pacific), the Japanese neritic waters and the neritic regions of the temperate Atlantic. *Muggiaea kochi* occupies the neritic tropico-equatorial Atlantic and the eastern equatorial Pacific (Alvariño, 1971).

Lensia challengeri is an Indo-Pacific species, and *L. fowleri* is most probably restricted to the Atlantic waters (Alvariño, 1971).

However, *Ch. appendiculata, M. kochi*, and *L. fowleri* appear widely distributed in the Caribbean region annex to the Panama Canal and in adjacent regions of the Caribbean, Gulf of Mexico, and western tropical Atlantic. *Ch. contorta, M. atlantica*, and *L. challengeri* appear in the Central American Pacific region. Few specimens of *Ch. appendiculata* and *M. kochi* were observed at locations near the opening of the Panama Canal in the Pacific, and few specimens of *Ch. contorta, M. atlantica*, and *L. challengeri* occurred at locations near the opening of the Panama Canal in the Caribbean. These observations suggest the Caribbean and the Pacific populations may be able to migrate or survive artificial transport via the Panama Canal (Figures 9-11, Table 2).

The species of siphonophores appearing abundantly distributed in the surveyed region in both the Caribbean and the Central American Pacific are *Diphyes bojani, D. dispar, Diphyopsis mitra*, and *A. eschscholtzi. Diphyes bojani* occurred at all Caribbean stations, except for the close to

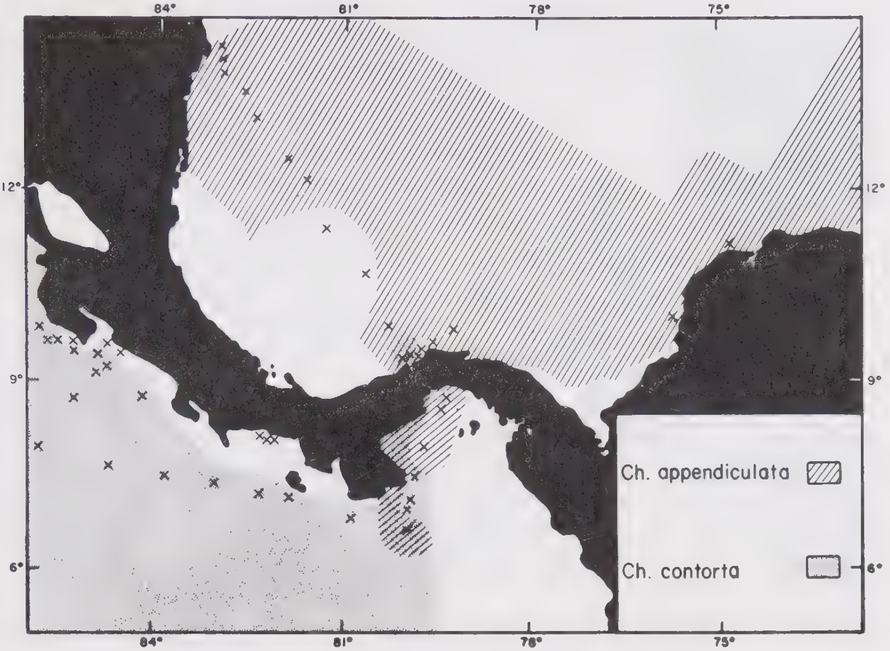
84°
81°
78°
75°
12°
9°
6°
Ch. appendiculata
Ch. contorta

FIGURE 9.—Distribution of *Chelophyes appendiculata* and *Chelophyes contorta* in the regions adjacent to the Panama Canal.

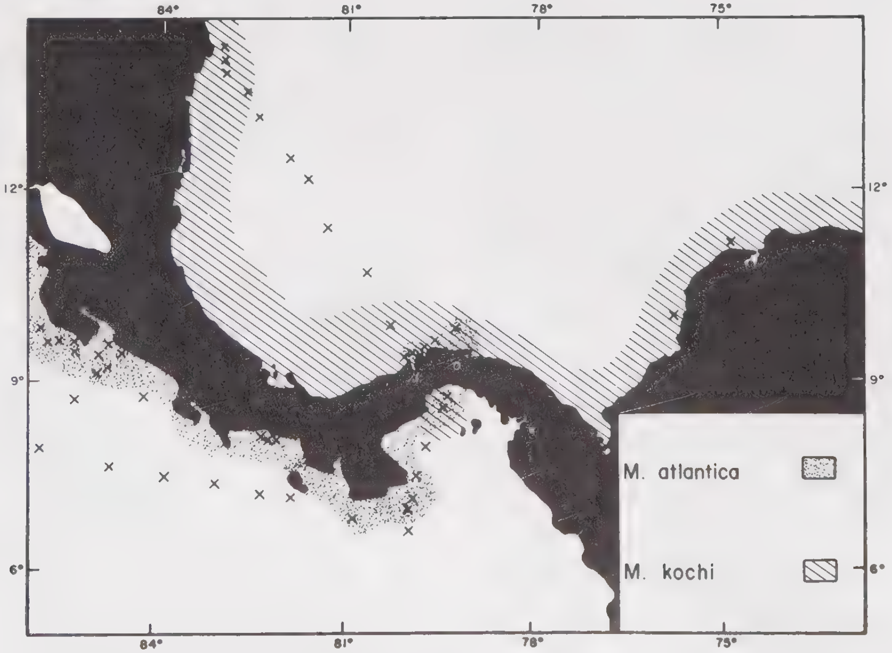
84°
81°
78°
75°
12°
9°
6°
M. atlantica
M. kochi

FIGURE 10.—Distribution of *Muggiaea atlantica* and *Muggiaea kochi* in the regions adjacent to the Panama Canal.

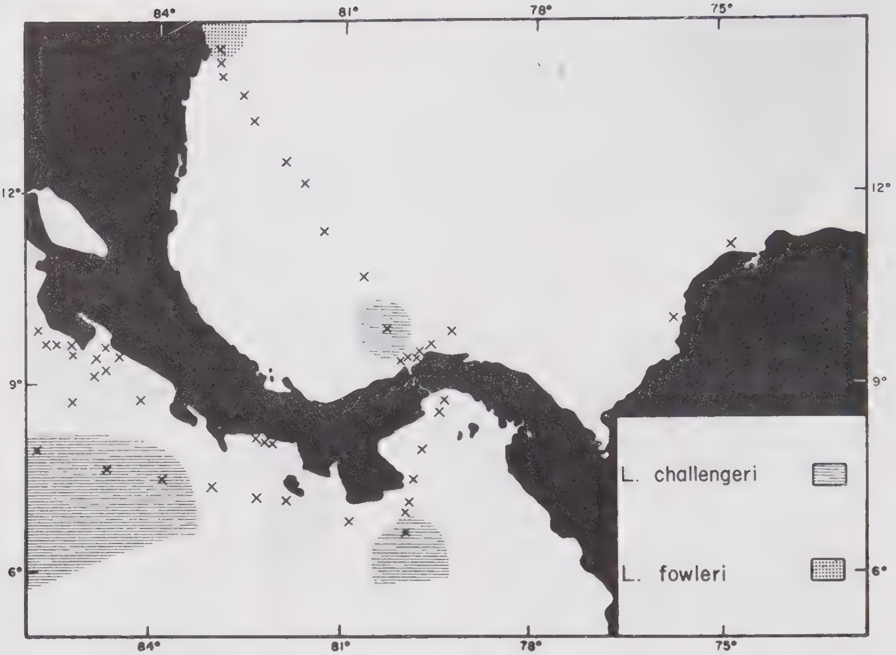

FIGURE 11.—Distribution of *Lensia challengeri* and *Lensia fowleri* in the regions adjacent to the Panama Canal.

shore locations off Huani, Nicaragua, off Puerto Colombia and Cartagena de Indias, and east to the entrance of the Panama Canal. In the Pacific region it was only missing at the northernmost station in the Gulf of Panama, south of Peninsula de Azuero, south of Coiba Island, off Gulf of Nicoya, and off Punta Arenas and Punta Guiones (Costa Rica) (Figure 12).

Diphyes dispar and *Diphyopsis mitra* appeared abundantly distributed in the Pacific region, and only in two locations in the Caribbean. *Diphyes dispar* was present off Colombia and off Laguna Perlas (Nicaragua), and *Diphyopsis mitra* at two locations a few miles north of Panama (Figures 12, 13).

Abylopsis eschscholtzi was only absent at a few stations in the Caribbean and in the Central American Pacific (Figure 14).

Species scattered distributed in both the Caribbean and the Pacific regions were *Eudoxoides spiralis, A. tetragona, S. chuni, A. okeni,* and *E. hyalinum. Eudoxides spiralis* was present only at five Caribbean locations, which include two stations off Nicaragua and three off the entrance to the Panama Canal, and in the Pacific appeared at two stations southeast of Peninsula de Azuero and at two offshore stations west of Costa Rica (Figure 13).

Abylopsis tetragona appeared off Colombia and near the entrance of the Panama Canal in the Caribbean, and south of the Azuero Peninsula, south of Coiba Island, west of Nicoya Peninsula, and at one offshore station west of Costa Rica in the Pacific (Figure 14).

Sulculeolaria chuni was observed at three locations over the deepest part of the western Caribbean, and in the Gulf of Panama, south of Nicoya Peninsula, and at two offshore stations west of Costa Rica in the Pacific (Figure 16).

Agalma okeni was found once in the Caribbean region (off Costa de Mosquitos, Nicaragua), and in the Pacific regions appeared from the Azuero Peninsula to Coiba Island, south of Costa Rica and west of Nicoya Peninsula (Figure 19).

Enneagonum hyalinum was only observed at the western Caribbean, and at several locations in the Pacific extending northwestwards from Coiba Island (Figure 17).

Species scattered distributed in the surveyed region of the Central American Pacific were, *S. quadrivalvis, S. turgida, B. bassensis,* and *H. hippopus* (Figures 16-18).

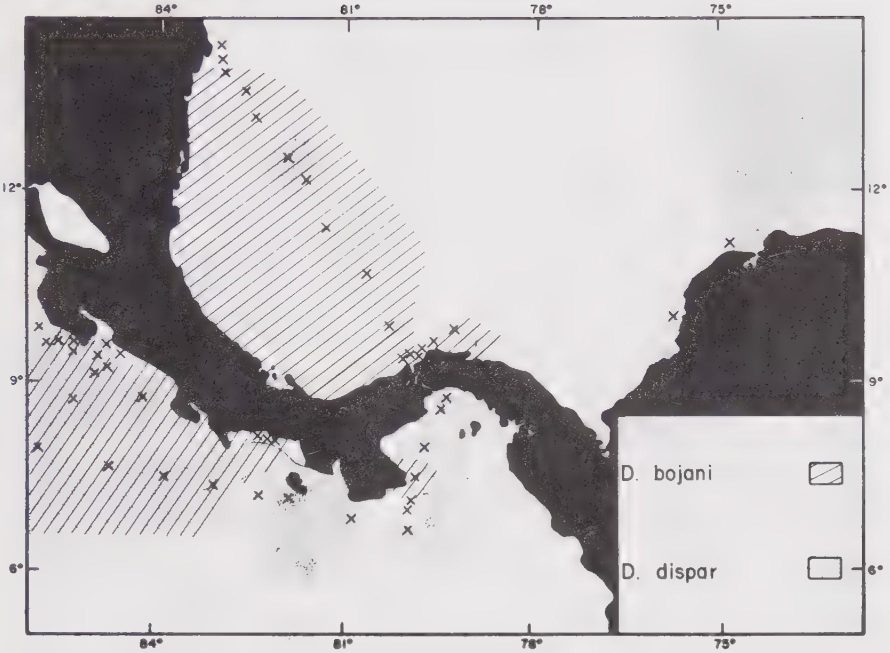
84°
81°
78°
75°
12°
9°
6°
D. bojani
D. dispar

FIGURE 12.—Distribution of *Diphyes bojani* and *Diphyes dispar* in the regions adjacent to the Panama Canal.

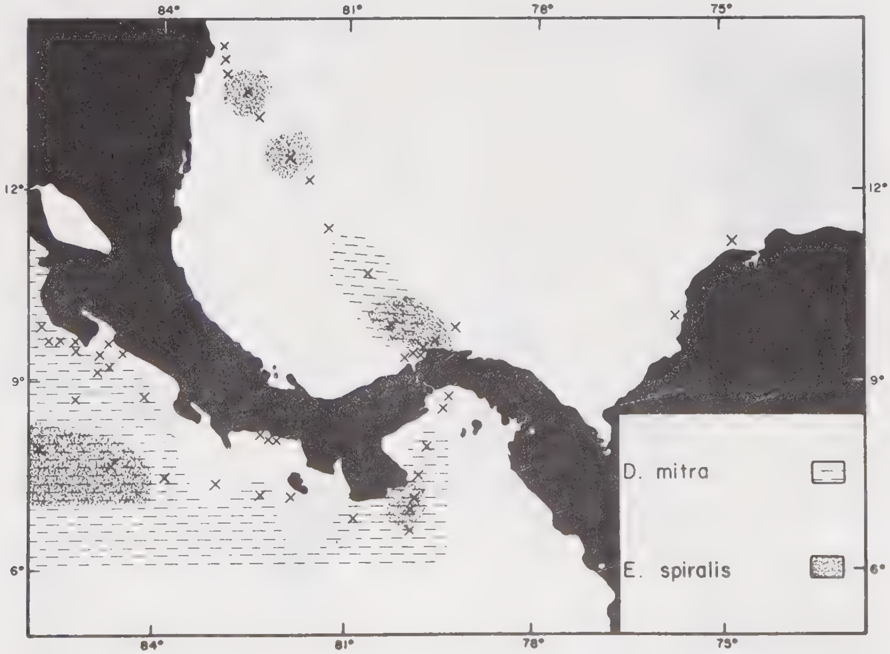
84°
81°
78°
75°
12°
9°
6°
D. mitra
E. spiralis

FIGURE 13.—Distribution of *Diphyopsis mitra* and *Eudoxoides spiralis* in the regions adjacent to the Panama Canal.

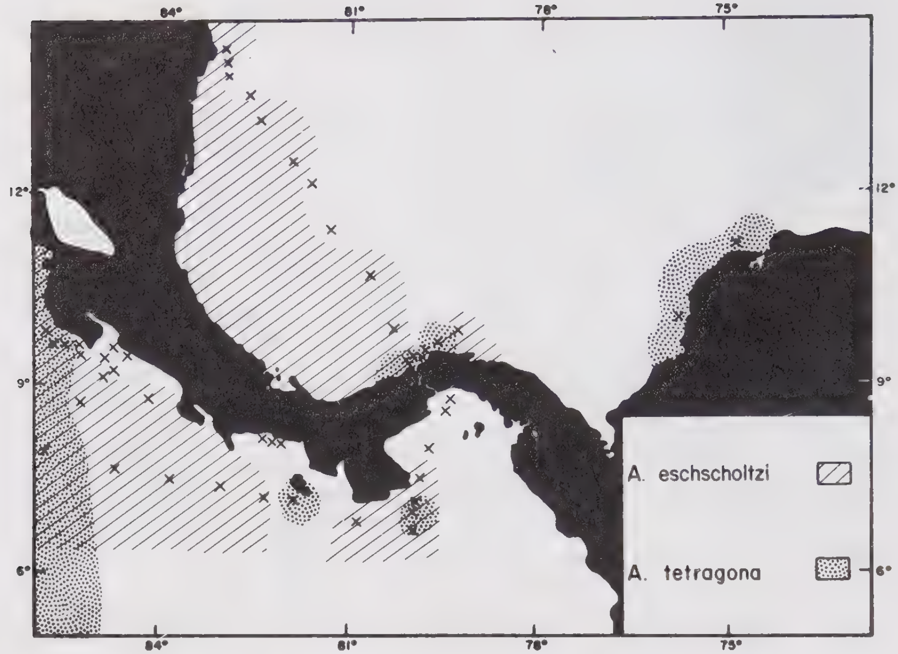
84°
81°
78°
75°
12°
9°
6°
A. eschscholtzi ▨
A. tetragona ▒

Figure 14.—Distribution of *Abylopsis eschscholtzi* and *Abylopsis tetragona* in the regions adjacent to the Panama Canal.

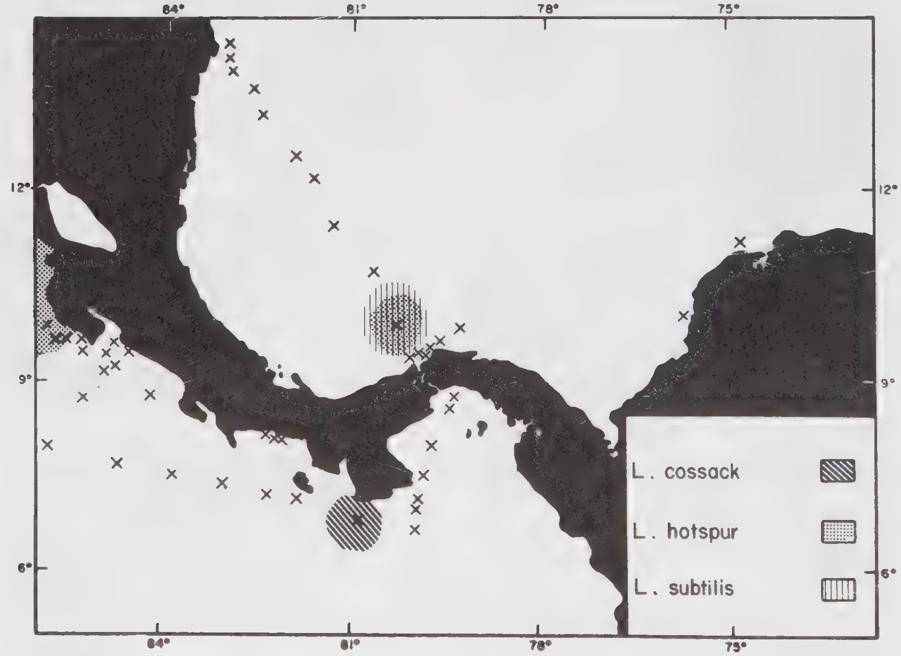
84°
81°
78°
75°
12°
9°
6°
L. cossack ▨
L. hotspur ▒
L. subtilis ▥

Figure 15.—Distribution of *Lensia cossack*, *Lensia hotspur*, and *Lensia subtilis* in the regions adjacent to the Panama Canal.

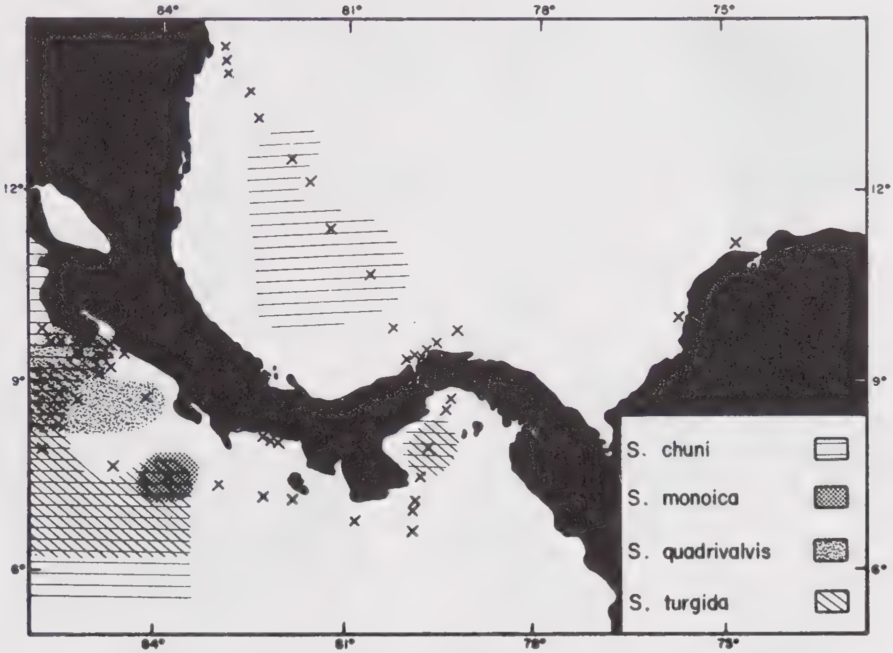
84°
81°
78°
75°
12°
9°
6°
S. chuni
S. monoica
S. quadrivalvis
S. turgida

FIGURE 16.—Distribution of *Sulculeolaria chuni*, *Sulculeolaria monoica*, *Sulculeolaria quadrivalvis*, and *Sulculeolaria turgida* in the regions adjacent to the Panama Canal.

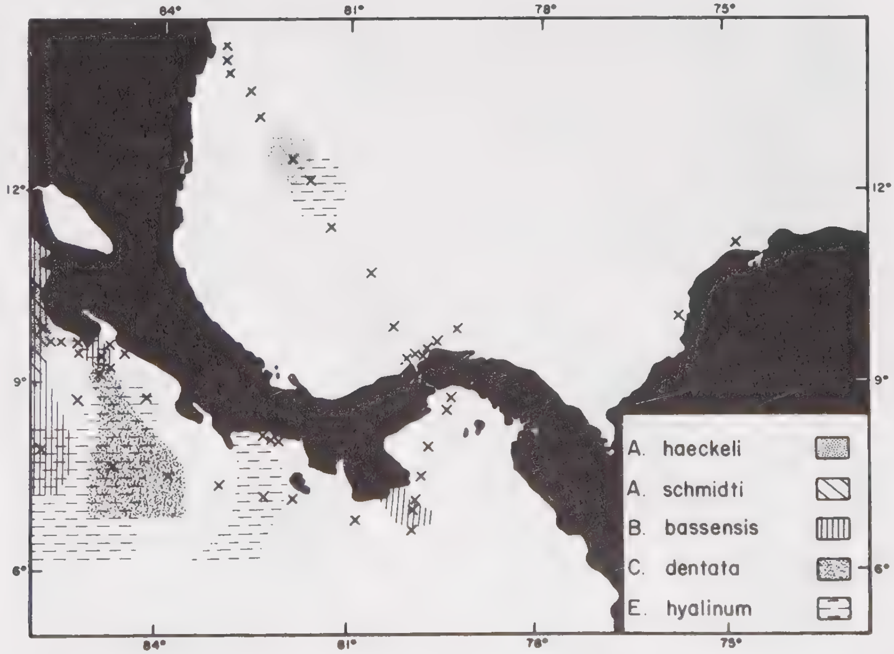
84°
81°
78°
75°
12°
9°
6°
A. haeckeli
A. schmidti
B. bassensis
C. dentata
E. hyalinum

FIGURE 17.—Distribution of *Abyla haeckeli*, *Abyla schmidti*, *Bassia bassensis*, *Ceratocymba dentata*, and *Enneagonum hyalinum* in the regions adjacent to the Panama Canal.

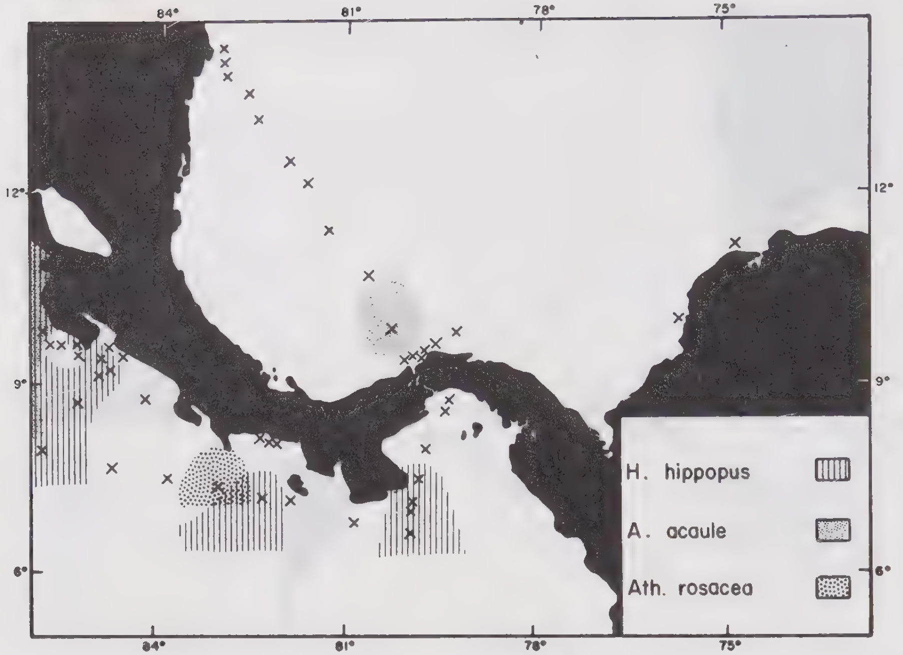
84°
81°
78°
75°
12°
9°
6°
H. hippopus
A. acaule
Ath. rosacea

FIGURE 18.—Distribution of *Hippopodius hippopus*, *Athoribya rosacea*, and *Amphicaryon acaule* in the regions adjacent to the Panama Canal.

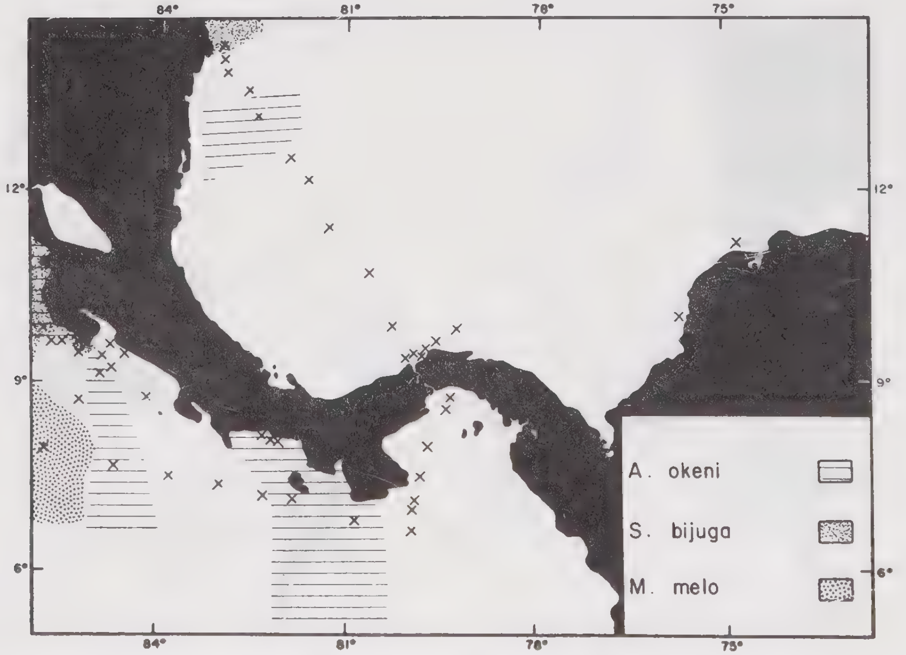
84°
81°
78°
75°
12°
9°
6°
A. okeni
S. bijuga
M. melo

FIGURE 19.—Distribution of *Agalma okeni*, *Stephanomia bijuga*, and *Melophysa melo* in the regions adjacent to the Panama Canal.

TABLE 1.—Siphonophores of the regions adjacent to the Suez Canal.

Species	Eastern Mediterranean	Red Sea
Chelophyes appendiculata Eschscholtz, 1829	• ••	
	32°20′N-34°51′E	Gulf of Elat:
	32°45′N-34°57′E	29°30′N-34°55′E
	33°03′N-34°55′E	29°25′N-34°50′E
	35°05′N-35°00′E	
	33°00′N-35°00′E	
	32°55′N-34°34′E	
	35°35′N-35°26′E	
	34°50′N-28°55′E	
	35°55′N-28°37′E	
	36°30′N-28°13′E	
	36°31′N-27°27′E	
	35°14′N-26°33′E	
	33°25′N-30°20′E	
	33°10′N-33°50′E	
	31°31′N-34°28′E	
	32°23′N-34°37′E	
	34°37′N-32°20′E	
	32°30′N-33°21′E	
	31°42′N-34°28′E	
	32°46′N-34°53′E	
	32°50′N-34°50′E	
	33°25′N-33°14′E	
	32°01′N-33°25′E	
	33°25′N-25°15′E	
	34°47′N-25°10′E	
	35°11′N-22°15′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	34°10′N-34°29′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	35°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
	35°55′N-28°33′E	
Eudoxia russelli Totton, 1932	35°57′N-32°23′E	Gulf of Elat:
		29°30°N-34°55′E
		29°25′N-34°50′E
Chelophyes contorta (Lens & Riemsdijk, 1908)	••	*+
	32°45′N-34°57′E	Gulf of Elat:
	35°05′N-35°00′E	29°25′N-34°50′E
	32°23′N-34°37′E	
	32°50′N-34°51′E	
	32°01′N-33°25′E	
	32°43′N-34°38′E	
Diphyes bojani (Eschscholtz, 1829)	••	
	36°31′N-27°27′E	
	33°25′N-30°20′E	
Diphyes chamissonis Huxley, 1859		+
Diphyes dispar Chamisso & Eysenhardt, 1821	••	+
	34°50′N-32°47′E	Gulf of Elat:
	35°05′N-35°00′E	29°30′N-34°55′E
	33°00′N-35°00′E	
	32°46′N-34°53′E	
	32°55′N-34°34′E	
	35°35′N-35°26′E	
	35°05′N-34°05′E	
	34°50′N-28°55′E	
	35°55′N-28°37′E	
	36°30′N-28°13′E	
	36°31′N-27°27′E	
	35°14′N-26°33′E	
	33°25′N-30°20′E	
	31°31′N-34°28′E	
	32°23′N-34°37′E	
	34°37′N-32°20′E	
	32°30′N-33°21′E	
	31°42′N-34°28′E	
(Diphyes dispar)	33°25′N-33°14′E	
	32°01′N-33°25′E	
	34°47′N-25°10′E	
	35°35′N-21°50′E	
	35°57′N-22°15′E	
	32°20′N-34°51′E	
	31°37′N-34°32′E	
	31°44′N-34°26′E	
	32°45′N-34°49′E	
	32°50′N-34°50′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	35°00′N-35°00′E	
	35°55′N-28°33′E	
Diphyopsis mitra Huxley, 1859		Gulf of Elat:
		29°30′N-34°55′E
Muggiaea atlantica Cunningham, 1892	• ••	+
Muggiaea kochi Will, 1844	• ••	
	33°03′N-34°55′E	
Eudoxoides spiralis Bigelow, 1911	• ••	
	35°05′N-35°00′E	
	31°31′N-34°28′E	
	34°37′N-32°20′E	
	32°50′N-34°51′E	
	34°35′N-29°40′E	
	34°10′N-34°29′E	
	35°57′N-32°23′E	
	34°35′N-33°35′E	
	35°05′N-34°38′E	
	33°50′N-31°15′E	
	32°43′N-34°48′E	
	32°10′N-32°50′E	
	32°07′N-33°24′E	
	31°42′N-33°00′E	
Clausophyes ovata Keferstein & Ehlers, 1861	••	
Sphaeronectes spp.	• ••	+
Lensia campanella Moser, 1925	••	+
	32°43′N-34°38′E	
	32°10′N-32°50′E	
	32°07′N-33°27′E	
Lensia conoidea Keferstein & Ehlers, 1861	• ••	
Lensia fowleri Bigelow, 1911	••	+
Lensia hotspur Totton, 1954		+
Lensia meteori Leloup, 1934	••	+
•	34°35′N-33°35′E	
	33°50′N-31°15′E	
Lensia multicristata Moser, 1925	• ••	
	32°45′N-34°49′E	
Lensia subtilis Chun, 1886	••	+
	34°35′N-29°40′E	Gulf of Elat:
	32°10′N-32°50′E	29°30′N-34°55′E
	32°07′N-33°24′E	29°25′N-34°50′E
Lensia subtiloides Lens & Riemsdijk, 1908	• ••	+
		Gulf of Elat:
		29°30′N-34°55′E
Sulculeolaria angusta Totton, 1954	35°05′N-35°00′E	
	32°55′N-34°34′E	
	32°46′N-34°53′E	
	37°17′N-22°47′E	
	35°11′N-22°15′E	
	34°35′N-29°40′E	
	32°07′N-33°24′E	
	35°00′N-35°00′E	
Sulculeolaria biloba Sars, 1846	• ••	

TABLE 1.—*Continued.*

Species	Eastern Mediterranean	Red Sea
Sulculeolaria chuni Lens & Riemsdijk, 1908	32°10′N-32°50′E 32°07′N-33°24′E 32°45′N-34°49′E	+ Gulf of Elat: 29°30′N-34°55′E
Sulculeolaria quadrivalvis Blainville, 1834	** 32°21′N-34°48′E 32°55′N-34°34′E 35°57′N-32°23′E 34°35′N-33°35′E 35°05′N-34°38′E 33°50′N-31°15′E	+ Gulf of Elat: 29°30′N-34°55′E 29°25′N-34°50′E
Sulculeolaria turgida (Gegenbauer, 1854)	** 32°45′N-34°49′E 35°35′N-35°26′E 34°47′N-25°10′E 35°35′N-21°50′E 35°57′N-22°15′E 34°35′N-29°40′E 34°10′N-34°29′E 35°57′N-32°23′E 34°35′N-33°35′E 35°05′N-34°38′E 33°50′N-31°15′E 32°43′N-34°38′E 32°10′N-32°50′E 35°00′N-35°00′E	
Abylopsis eschscholtzi Huxley, 1859	* **	+ Gulf of Elat: 29°25′N-34°50′E
Abylopsis tetragona Otto, 1823	* ** 33°25′N-30°20′E 35°05′N-34°38′E 32°10′N-32°50′E	+ Gulf of Elat: 29°30′N-34°55′E 29°25′N-34°50′E
Bassia bassensis Quoy & Gaimard, 1834	* ** 33°03′N-34°55′E 33°25′N-30°20′E 31°31′N-34°28′E 32°23′N-34°37′E 32°30′N-33°21′E 35°11′N-22°15′E 35°57′N-22°15′E 34°35′N-29°40′E 34°10′N-34°29′E 32°46′N-34°53′E 35°57′N-32°23′E 34°35′N-33°35′E 35°05′N-34°38′E 33°50′N-31°15′E 32°43′N-34°48′E 32°10′N-32°50′E 32°07′N-33°24′E 31°42′N-33°00′E 31°37′N-34°32′E 35°55′N-28°33′E	+
Ceratocymba sagittata Quoy & Gaimard, 1827	**	
Enneagonum hyalinum Quoy & Gaimard, 1827	* **	+ Gulf of Elat: 29°25′N-34°50′E
Hippopodius hippopus Forskal, 1776	* ** 32°21′N-34°48′E 35°39′N-26°34′E 35°05′N-35°00′E 32°23′N-34°37′E 32°55′N-34°34′E 35°35′N-35°26′E 35°05′N-34°05′E 34°50′N-28°55′E 35°55′N-28°37′E 36°31′N-27°27′E 32°46′N-34°53′E 33°25′N-33°14′E 32°01′N-33°25′E 34°47′N-25°10′E 33°25′N-25°15′E 37°17′N-22°47′E 35°11′N-22°15′E 35°35′N-21°50′E 35°57′N-22°15′E 34°35′N-29°40′E 34°10′N-34°29′E 32°50′N-34°50′E 32°20′N-34°51′E 31°37′N-34°32′E 31°42′N-34°28′E 31°44′N-34°26′E 32°45′N-34°49′E 34°35′N-33°35′E 35°05′N-34°38′E 33°50′N-31°15′E 32°43′N-34°38′E 32°10′N-32°50′E 32°07′N-33°24′E 31°42′N-33°00′E 35°00′N-35°00′E 35°55′N-28°33′E	+
Vogtia glabra Bigelow, 1918	* **	
Vogtia pentacantha Kolliker, 1853	**	
Vogtia spinosa Keferstein & Ehlers, 1861	**	
Praya cymbiformis Chiaje, 1841	**	
Rosacea plicata Quoy & Gaimard, 1827	** 32°10′N-32°50′E	
Amphicaryon acaule Chun, 1888	**	+
Amphicaryon ernesti Totton, 1954		+
Anthophysa rosea Brandt, 1835	**	+
Apolemia uvaria Lesueur, 1811	** 36°31′N-27°27′E	
Rhizophysa filiformis Forskal, 1775	**	
Cordagalma cordiformis Totton, 1932	**	+ 29°25′N-34°50′E
Athoribya rosacea (Forskal, 1775)	**	+ 29°25′N-34°50′E
Agalma elegans Sars, 1846	* ** 35°55′N-28°33′E	+ Gulf of Elat: 29°30′N-34°55′E 29°25′N-34°50′E
Agalma okeni Eschscholtz, 1825	* **	+ Gulf of Elat: 29°30′N-34°55′E 29°25′N-34°50′E
Stephanomia bijuga (Chiaje, 1841-42)	* **	+
Stephanomia rubra Vogt, 1852	* **	+
Nanomia cara Agassiz, 1865	**	
Physophora hydrostatica Forskal, 1775	** 35°57′N-22°45′E 34°35′N-29°40′E 35°50′N-31°15′E 31°42′N-33°00′E	
Forskalia edwardsi Kolliker, 1853	* **	+

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* Previously observed (see Alvariño, 1971; Lakkis, 1971).
+ Previously observed in the Red Sea (Alvariño, 1971 compilation of distributional data).
**Previously observed in the western Mediterranean (see Alvariño, 1971).

TABLE 2.—Siphonophores of the regions adjacent to the Panama Canal.

Species	Caribbean Sea region	Central American Pacific	Species	Eastern Mediterranean	Red Sea
Chelophyes appendiculata	• ••		*(Diphyopsis mitra)*		07°12′N-79°54′W
	11°07′N-74°47′W	08°41′N-79°31′W			07°02′N-79°57′W
	10°19′N-75°38′W	08°48′N-79°30′W			06°40′N-79°59′W
	09°46′N-79°20′W	08°00′N-79°43′W			06°55′N-80°50′W
	09°37′N-79°39′W				07°18′N-82°25′W
	09°27′N-79°48′W				07°30′N-83°54′W
	14°19′N-83°09′W				07°39′N-84°46′W
	13°56′N-82°59′W				07°57′N-85°49′W
	13°38′N-82°38′W				08°48′N-85°57′W
	13°12′N-82°25′W				09°07′N-84°58′W
	12°31′N-81°52′W				09°32′N-85°10′W
	12°11′N-81°38′W				09°51′N-85°43′W
	10°04′N-80°22′W		*Muggiaea atlantica*		••
Chelophyes contorta		••		09°28′N-84°21′W	09°38′N-85°44′W
	09°27′N-79°48′W	07°30′N-79°54′W		09°46′N-79°20′W	08°41′N-79°31′W
	09°25′N-79°57′W	08°46′N-84°11′W		09°27′N-79°48′W	07°30′N-79°54′W
		09°13′N-84°45′W			08°10′N-82°13′W
		09°28′N-85°15′W			08°10′N-82°15′W
		09°39′N-85°41′W			08°10′N-82°16′W
		07°12′N-79°54′W			09°13′N-84°45′W
		07°02′N-79°57′W			09°28′N-85°15′W
		06°55′N-80°50′W			09°39′N-85°41′W
		07°12′N-81°48′W			08°48′N-79°30′W
		07°18′N-82°25′W			07°12′N-79°54′W
		07°27′N-83°04′W			07°02′N-79°57′W
		07°30′N-83°54′W			06°55′N-80°50′W
		07°39′N-84°46′W			09°07′N-84°58′W
		07°51′N-85°49′W			09°23′N-84°52′W
		08°48′N-85°17′W			09°39′N-84°44′W
		09°07′N-84°58′W			09°32′N-85°10′W
		09°23′N-84°52′W			09°51′N-85°43′W
		09°51′N-85°43′W	*Muggiaea kochi*	••	
Dimophyes arctica	••	••		11°07′N-74°47′W	08°41′N-79°31′W
(Chun, 1897)				10°19′N-75°38′W	
Diphyes bojani	••	••		09°46′N-79°20′W	
	09°46′N-46°20′W	07°30′N-79°54′W		09°37′N-79°39′W	
	09°27′N-79°47′W	08°10′N-82°13′W		09°28′N-79°46′W	
	09°27′N-79°38′W	08°10′N-82°15′W		09°27′N-79°47′W	
	13°56′N-82°59′W	08°10′N-82°16′W		14°19′N-83°09′W	
	13°38′N-82°38′W	08°46′N-84°11′W		14°07′N-83°01′W	
	13°12′N-82°25′W	09°13′N-84°45′W		13°56′N-82°59′W	
	12°31′N-81°52′W	09°28′N-85°15′W		13°38′N-82°38′W	
	12°11′N-81°38′W	09°39′N-85°41′W		10°04′N-80°22′W	
	11°27′N-81°15′W	07°27′N-83°04′W		09°25′N-79°57′W	
	10°44′N-80°45′W	07°30′N-83°54′W	*Eudoxoides spiralis*	••	••
	10°04′N-80°22′W	07°39′N-84°46′W		09°37′N-79°39′W	07°12′N-79°54′W
		07°57′N-85°49′W		09°28′N-79°46′W	07°02′N-79°57′W
		08°48′N-85°17′W		13°38′N-82°38′W	07°39′N-84°46′W
		09°07′N-84°58′W		12°31′N-81°52′W	07°57′N-85°49′W
		09°23′N-84°52′W		10°04′N-80°22′W	
Diphyes dispar	• ••	• ••	*Lensia campanella*	••	••
	10°19′N-75°38′W	09°38′N-85°44′W	*Lensia challengeri*		••
	08°46′N-84°11′W	08°48′N-79°30′W	Totton, 1954	10°04′N-80°22′W	06°40′N-79°59′W
	09°13′N-84°45′W	08°00′N-79°43′W			07°30′N-83°54′W
	09°28′N-85°15′W	06°40′N-79°59′W			07°39′N-84°46′W
	09°39′N-85°41′W	06°55′N-80°50′W			07°57′N-85°49′W
	12°31′N-81°52′W	07°12′N-81°48′W	*Lensia conoidea*		••
		07°27′N-83°04′W	*Lensia cossack* Totton, 1941	••	••
		07°30′N-83°54′W			06°55′N-80°50′W
		07°39′N-84°36′W	*Lensia fowleri*	••	
		07°57′N-85°49′W		14°19′N-83°09′W	
		08°48′N-85°17′W	*Lensia hotspur*	••	••
		09°07′N-84°58′W		10°04′N-80°22′W	09°51′N-85°43′W
		09°23′N-84°52′W	*Lensia lelouveteau*	••	
		09°39′N-84°44′W	Totton, 1941		
		09°32′N-85°10′W	*Lensia meteori*		••
		09°51′N-85°43′W	*Lensia multicristata*	••	
Diphyopsis mitra	••	••	*Lensia reticulata*	••	
	10°44′N-80°45′W	07°30′N-79°54′W	Totton, 1954		
	10°04′N-80°22′W	08°46′N-84°11′W	*Lensia subtilis*	• ••	
		09°13′N-84°45′W		10°04′N-80°22′W	
		09°28′N-85°15′W	*Sulculeolaria bigelowi*		••
		09°39′N-85°41′W	(Sears, 1950)		
		08°00′N-79°43′W	*Sulculeolaria biloba*	••	••

TABLE 2.—*Continued.*

Species	Eastern Mediterranean	Red Sea
Sulculeolaria chuni	** 12°31′N-81°52′W 11°27′N-81°15′W 10°44′N-80°45′W	** 08°00′N-79°13′W 07°30′N-83°54′W 07°57′N-85°49′W 09°23′N-84°52′W
Sulculeolaria monoica Chun, 1888	**	** 07°30′N-83°54′W
Sulculeolaria quadrivalvis	**	** 08°46′N-84°11′W 09°28′N-85°15′W 08°48′N-85°17′W 09°07′N-84°58′W 09°23′N-84°52′W
Sulculeolaria turgida		** 08°00′N-79°43′W 07°30′N-83°54′W 07°57′N-85°49′W 09°23′N-84°52′W
Abyla carina Haeckel, 1888	**	
Abyla haeckeli Lens & Riemsdijk, 1908	* ** 12°31′N-81°52′W	* ** 09°51′N-85°43′W
Abyla schmidt Sears, 1953	**	09°51′N-85°43′W
Abylopsis eschscholtzi	* ** 10°46′N-79°20′W 14°19′N-83°09′W 14°07′N-83°01′W 13°12′N-82°25′W 12°31′N-81°52′W 10°44′N-80°45′W 10°04′N-80°22′W 09°25′N-79°57′W	* ** 07°30′N-79°54′W 08°46′N-84°11′W 09°28′N-85°15′W 09°39′N-83°09′W 07°12′N-97°54′W 07°02′N-79°57′W 06°40′N-79°59′W 06°55′N-80°50′W 07°18′N-82°25′W 07°27′N-83°04′W 07°30′N-83°54′W 07°39′N-84°46′W 07°57′N-85°49′W 08°48′N-85°17′W 09°07′N-84°58′W 09°51′N-85°43′W
Abylopsis tetragona	* ** 11°07′N-74°47′W 10°19′N-75°38′W 09°37′N-79°39′W 09°25′N-79°57′W	09°38′N-85°44′W 07°02′N-79°57′W 07°57′N-85°49′W 09°51′N-85°43′W
Bassia bassensis	**	* ** 07°02′N-79°57′W 07°57′N-85°49′W 09°23′N-84°52′W 09°51′N-85°43′W
Ceratocymba dentata Bigelow, 1918		* ** 07°30′N-83°54′W 07°39′N-84°46′W 09°07′N-84°58′W
Ceratocymba leuckarti Huxley, 1859	**	**
Ceratocymba sagittata	**	
Enneagonum hyalinum	** 12°11′N-81°38′W	* ** 07°18′N-82°25′W 08°46′N-84°11′W 07°39′N-84°46′W 07°57′N-85°49′W 09°07′N-84°58′W 09°23′N-84°52′W 09°32′N-85°10′W
Hippopodius hippopus	**	** 07°30′N-79°54′W 07°12′N-79°54′W 07°02′N-79°57′W 06°42′N-79°59′W 07°18′N-82°25′W 07°57′N-85°49′W 08°48′N-85°17′W 09°07′N-84°58′W 09°23′N-84°52′W 09°32′N-85°10′W 09°51′N-85°43′W
Vogtia glabra	**	
Vogtia pentacantha	**	
Vogtia spinosa		**
Rosacea plicata		**
Nectopyramis natans Bigelow, 1911		**
Amphicaryon acaule	* ** 10°04′N-80°22′W	** 09°51′N-85°43′W
Amphicaryon ernesti	**	
Rhizophysa filiformis	**	
Athoribya rosacea		07°27′N-83°04′W
Agalma elegans	**	
Agalma okeni	** 13°12′N-82°25′W	* ** 06°55′N-80°50′W 07°12′N-81°48′W 07°39′N-84°46′W 09°07′N-84°58′W 09°32′N-85°10′W 09°51′N-85°43′W
Stephanomia bijuga	** 14°19′N-83°09′W	** 09°32′N-85°10′W 09°51′N-85°43′W
Stephanomia rubra	**	
Physophora hydrostatica		**
Melophysa melo Quoy & Gaimard, 1827		* 07°57′N-85°49′W

*Previously observed.
**Previously observed in adjacent regions of the Caribbean Sea and/or the Gulf of Mexico, and adjacent regions of the Pacific Ocean (see Alvariño, 1971 compilation of distributional data).

Species present at few locations in the surveyed region of the Caribbean and Pacific were, *L. hotspur*, *Abyla haeckeli*, and *A. acaule*. *Lensia hotspur* and *A. acaule* were only found at one location to the north off the entrance of the Panama Canal in the Caribbean, and west of the Peninsula de Nicoya in the Pacific (Figures 15, 18). *Abyla haeckeli* was observed once off Costa de Mosquitos, Caribbean Sea, and at one location off Punta Guiones in the Pacific (Figure 17).

Species present once or at few locations in the Pacific region were, *L. cossack*, *S. monoica*, *Abyla schmidti*, *C. dentata*, *Melophysa melo*, *A. rosacea*, and *Stephanomia bijuga* (Figures 15-19).

Lensia subtilis and *L. fowleri* were found only once each, respectively at few miles north of the entrance to the Panama Canal, and off Huani in the Caribbean (Figures 11, 15).

The information presented here should be considered only as a basis for future and more detailed sets of investigations to enlighten further the distribution and the characteristics of the populations of siphonophores, their fluctuations in time and locations, concurrently with the hydrographic, ecological characteristics and other variants.

The author regrets that the pertinent hydrographic data obtained concurrently with the zooplankton collections were not available in time to be included in the discussion of results.

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MIGRATIONS OF YELLOWFIN TUNA TAGGED OFF THE SOUTHERN COAST OF MEXICO IN 1960 AND 1969

by

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ABSTRACT

The map method, the Jones method, the variance-covariance method, and the Skellam method were used to study the migrations of tagged yellowfin tuna released off the southern coast of Mexico in 1960 and 1969. The first three methods are all useful, and each presents information which is complementary to that presented by the others. The Skellam method, as used in this report, is less useful.

The movements of the tagged fish released in 1960 appeared to have been strongly directed, but this was probably caused principally by the distribution of the fishing effort. The effort was much more widely distributed in 1970, and the movements of the fish released in 1969 appeared to have been much less directed. The correlation coefficients derived from the variance-covariance method showed that it was not random, however.

The small fish released in the Acapulco and 10°N-100°W areas in 1969 migrated to the Manzanillo area near the beginning of February 1970. The medium and large fish released in the same areas in the same year tended to migrate to the southeast throughout the first half of 1970, however.

INTRODUCTION

The migrations of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean have been studied by Blunt and Messersmith (1960), Schaefer, Chatwin, and Broadhead (1961), and Fink and Bayliff (1970), the last report including data on all tagged fish released prior to 1965. Almost all the tagging of yellowfin off the southern Mexico coast up to that time was accomplished on two cruises conducted in 1960. During the middle and late 1960's the fishery expanded offshore, particularly between the equator and 15°N (Calkins and Chatwin, 1967 and 1971), and during the periods of restricted fishing for yellowfin inside the Tuna Commission's yellowfin regulatory area (CYRA) (Figure 1) fishing has been conducted to the west of this area. For this reason additional tagging was conducted off the southern Mexico coast during 1969, both near the coast and far offshore. This report constitutes an analysis of the 1960 and 1969 experiments, using some new techniques in addition to those employed in the previous reports.

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The indispensable cooperation of the fishing vessel captains and fishermen, and of cannery workers, in returning the tags when the fish were recovered, together with pertinent information, is also acknowledged with gratitude.

The computer programs used in this report were written or modified by Dr. Robert C. Francis, Miss JoAnne Levatin, and Messrs. Christopher T. Psaropulos and Donald L. Whitt. The manuscript was reviewed by Drs. James Joseph, Robert C. Francis, and Jerome J. Pella.

MATERIALS AND METHODS

The methods of tagging the fish and handling the tag return data are described by Fink (1965), Fink and Bayliff (1970), and Bayliff (1973). The methods of collecting and handling the catch and effort statistics are discussed by Shimada and Schaefer (1956), Joseph and Calkins (1969), and Bayliff (1971).

Most of the calculations were performed on the CDC 3600 and Burroughs 6700 computers at the University of California at San Diego. Programs CIAT F04 (Psaropulos, 1966) and two unpublished programs were employed for this purpose.

DATA EMPLOYED

Tag releases and returns

The data for only three cruises are used in this report, as no more than nine tag returns have resulted from any other cruises conducted in this area. The release and return data for these cruises are listed in Table 1. Not all of the return data were used, as some were unsuitable because the area or date of recapture was unknown or for some other reason. Some tagging has been conducted near the Revillagigedo Islands and near Clipperton Island, but these fish behave differently from those tagged further away from the islands, many of them apparently staying near the islands for considerable lengths of time (Fink and Bayliff, 1970). Since most of the catch off the southern Mexico coast is made in areas not in the vicinity of these islands, the data for the tagging experiments conducted near these islands are not considered in this report. The areas where the tagged fish were released are shown in Figure 2.

Statistics of the fishery

The statistical data routinely collected by the Tuna Commission include the logged catches in short tons of yellowfin by 1-degree and 5-degree areas, by months, quarters, and years, by types of gear (purse seine and baitboat), and by size classes of vessels, and the corresponding effort in days of fishing, both unstandardized and standardized to Class-3 purse-seine (vessels of 101-200 short tons capacity) days and Class-4 baitboat (vessels of 201-300 short tons capacity) days (Shimada and Schaefer, 1956; Joseph and Calkins, 1969). The effort data obtained by the Tuna Commission represent about 90 percent of the total effort for the periods in question, and are assumed to have the same distribution by area and time as the total effort. In each year since 1966 there has been a quota on the catch of yellowfin in the CYRA, and most of the vessels which leave port after the closure date each year are restricted as to the portion of the fish landed from their catches made inside the CYRA which can be yellowfin. The effort exerted inside the CYRA by vessels which leave port after the closure date is termed "regulated effort," and these data are kept separately from the "unregulated effort" data. All unregulated effort is assumed to be directed toward yellowfin (and also toward skipjack) except that for the few trips for which species other than yellowfin or skipjack make up more than one third of the total weight of the catch. The regulated effort data are not used in this study.

It is necessary to obtain estimates of the fishing effort in each 5-degree area-month stratum in which tagged fish were recaptured. The effort data were all converted to Class-3 purse-seine units by the method of Bayliff (1971), using separate baitboat catch-per-unit-of-effort data for 0°-15°N and north of 15°N. The monthly effort for purse seiners and baitboats, and for both gears combined, for the areas where tagged fish were recaptured are shown for March 1960-May 1961 in Table 2 and January-December 1970 in Table 3. The 5-degree areas are coded by the latitudes and longitudes at their southeast corners, preceded by 0's for areas north of the equator or 2's for areas south of the equator (Shimada and Schaefer, 1956). There was no unregulated effort inside the CYRA during October-December 1969, and all but one of the tag returns for this period were from fish recaptured by the tagging vessel.

RESULTS

The area-time strata in which tagged fish are recaptured depend not only upon the migrations of the fish, but also upon the distribution of the fishing effort. If a tagged fish is released in one area the probability of its being recaptured in another depends not only upon the fishing effort in the second area, but also upon that in the first area and in all the areas through which the fish passes while traveling from the first to the second area. Most of the analyses of migrations of the tagged fish in this report are performed two ways, without and with adjustments for the differences in the amounts of fishing effort in the different 5-degree area-month strata of recapture. These adjustments were accomplished by dividing the number of returns for each 5-degree area-month stratum by the corresponding effort and then multiplying it by a factor to get an adjusted number of returns. The calculations are explained in detail in later sections of this report.

The method of adjustment is inadequate, as no allowance is made for the amounts of fishing effort in the area-time strata through which the fish passed prior to their recapture. Such adjustments could probably be accomplished only by computer simulation. In the meantime, however, the adjustment just described is probably better than none at all.

Methods involving maps

The locations of recapture of the fish from each group of releases are shown in Figure 2. These maps give a useful impression of the distances and directions traveled, but do not express these parameters in quantitative terms. Furthermore, there is no provision for indicating the dates of recapture or times at liberty, and this could be done only by substituting several maps for each of the present maps.

In Figure 3 and Table 4 are shown the adjusted numbers of returns in eight arbitrarily-chosen areas for fish released in a 15-degree area (Area A in the figure) in 1969. These were calculated by

$$N_{ij} = \left(\frac{n_{ij}}{f_{ij}}\right)\left(\frac{\sum_i \sum_j n_{ij}}{\sum_i \sum_j \frac{n_{ij}}{f_{ij}}}\right) \qquad (1)$$

where

N_{ij} = adjusted number of returns in area i during month j,
n_{ij} = actual number of returns in area i during month j, and
f_{ij} = effort in area i during month j.

The four returns of fish released north of 20°N were not used for these calculations, but six returns for which the 5-degree areas of recapture, but not the 1-degree areas of recapture, were known were used. It is clear that relatively few tagged fish released in the 15-degree area in question migrated to the areas west of Baja California, outside the CYRA, or south of 5°N. For these data it appears that tagged fish released in Area A moved from Area A to Area 2 near the beginning of February and back to

Area A near the end of that month. The incidence of tagged fish released in Area A increased in Area B from January to May, indicating movement of fish released in Area A to Area B during this period.

Skellam method

The averages of the squared distances of movement are calculated by

$$\overline{r_j^2} = \left(\sum^{n_j} r_j^2\right) \Big/ n_j \tag{2}$$

where

$\overline{r_j^2}$ = average of the squared distances of movement by fish recaptured in month j,

r_j = distance of movement by fish recaptured in month j, and

n_j = number of returns for fish recaptured in month j.

The adjusted averages of the squared distances of movement are calculated by

$$\overline{R_j^2} = \sum^{n_j}\left(\frac{r_{ij}^2}{f_{ij}}\right) \Big/ \sum^{n_j}\left(\frac{1}{f_{ij}}\right) \tag{3}$$

R_j^2 = adjusted average of the squared distances of movement by fish recaptured in month j,

r_{ij} = distance of movement by fish recaptured in area i during month j, and

f_{ij} = effort in area i during month j.

Skellam (1951) pointed out that if the dispersion is random the averages of the squared distances of movement increase linearly with time. If the point of release is near the coast, however, the fish can go only a short distance in that direction, and the rate of dispersion will appear to decrease with time even if such is not the case.

The unadjusted averages of the squared distances of movement for the six groups of releases in question are shown on the left side of Figure 4. The points are plotted only for the months which include at least five returns. The numbers near the points indicate the numbers of returns in each month. These data indicate that the dispersion is roughly random. For the Manzanillo area the number of returns was relatively high and the $\overline{r_j^2}$ value was relatively low for February 1970, whereas the reverse was true for the Acapulco and 10°N-100°W areas. This is probably because the effort was relatively high in the 0-15-105 and 0-20-105 areas and relatively low in 0-10-095, 0-10-100, and 0-10-105 areas during that month (Table 4).

The adjusted averages of the squared distances of movement are shown on the right side of Figure 4. These graphs are quite similar to those on the left side of the figure. The $\overline{R_j^2}$ values for February 1970 for the Acapulco and 10°N-100°W areas are relatively high, which indicates that on the average the fish were further away from the areas of release during February than during January or March. The data indicate the presence of fish from those two areas in the Manzanillo area during February, so it is logical to assume that the high effort exerted in that area during that month was due at least partly to an influx of fish from the Acapulco and 10°N-100°W areas.

If the movement is mostly or entirely in one direction and at a constant rate the average distances of movement increase linearly with time, and the averages of the squared distances of movement increase exponentially. It will be shown in the next section that the fish of the 1960 releases which were recaptured moved mostly in one direction, and it can be seen that the graphs for the fish released in the Acapulco area in 1960 are concave upward and thus roughly exponential.

Jones method

This method, devised by Jones (1959 and 1966), has been used previously in a slightly different form for yellowfin by Fink and Bayliff (1970).

The dispersion of the fish is analyzed from data on the months of recapture, days at liberty, distances of movement, and directions of movement. Eight directions of movement, 0°-45° true = 0, 45°-90° true = 1, . . . , and 315°-360° true = 7, are used.

For the unadjusted data the following calculations are made by month of recapture, by all months of recapture combined, by direction of movement, and by all directions of movement combined

$$\overline{t_{jk}} = \sum^{n_{jk}} t_{jk} \Big/ n_{jk} \qquad (4)$$

where

$\overline{t_{jk}}$ = average time at liberty for fish recaptured in month j which had moved in direction k,

t_{jk} = time at liberty for fish recaptured in month j which had moved in direction k, and

n_{jk} = number of fish recaptured in month j which had moved in direction k,

$$\overline{r_{jk}} = \sum^{n_{jk}} r_{jk} \Big/ n_{jk} \qquad (5)$$

where

$\overline{r_{jk}}$ = average distance of movement for fish recaptured in month j which had moved in direction k and

r_{jk} = distance of movement for fish recaptured in month j which had moved in direction k,

$$v_{jk} = \frac{\sqrt{\left(\sum^{n_{jk}} r_{jk} \sin \Theta_k\right)^2 + \left(\sum^{n_{jk}} r_{jk} \cos \Theta_k\right)^2}}{\sum^{n_{jk}} t_{jk}} \qquad (6)$$

where

v_{jk} = mean velocity of dislocation for fish recaptured in month j which had moved in direction k and

Θ_k = angle corresponding to direction of movement k (Direction 0 = 67½°, Direction 1 = 22½°, Direction 2 = 337½°, . . . , and Direction 7 = 112½°), and

$$a_{jk}^2 = \frac{1}{n_{jk}} \left[\sum^{n_{jk}} \frac{r_{jk}^2}{t_{jk}} - \frac{\left(\sum^{n_{jk}} r_{jk} \sin \Theta_k\right)^2 + \left(\sum^{n_{jk}} r_{jk} \cos \Theta_k\right)^2}{\sum^{n_{jk}} t_{jk}} \right] \qquad (7)$$

where

a_{jk}^2 = mean square dispersion coefficient for fish recaptured in month j which had moved in direction k.

The adjusted number of returns in each month-direction of movement stratum is calculated by

$$N_{jk} = \left(\sum_i^{n_{jk}} \frac{n_{ijk}}{f_{ij}}\right) \left(\frac{\sum_i \sum_j \sum_k n_{ijk}}{\sum_i \sum_j \sum_k \frac{n_{ijk}}{f_{ij}}}\right) \qquad (8)$$

where

N_{jk} = adjusted number of returns in month j for fish which had moved in direction k,

n_{ijk} = actual number of returns in area i during month j for fish which had moved in direction k, and

f_{ij} = effort in area i during month j.

The calculations analogous to those performed by Formulae (4), (5), (6), and (7) are accomplished by

$$\overline{T_{jk}} = \sum_{i}^{n_{jk}} \left(\frac{t_{ijk}}{f_{ij}}\right) \Bigg/ \sum_{i}^{n_{jk}} \left(\frac{1}{f_{ij}}\right) \tag{9}$$

where

$\overline{T_{jk}}$ = adjusted average time at liberty for fish captured in month j which had moved in direction k and

t_{ijk} = time at liberty for fish recaptured in area i during month j which had moved in direction k,

$$\overline{R_{jk}} = \sum_{i}^{n_{jk}} \left(\frac{r_{ijk}}{f_{ij}}\right) \Bigg/ \sum_{i}^{n_{jk}} \left(\frac{1}{f_{ij}}\right) \tag{10}$$

where

$\overline{R_{jk}}$ = adjusted average distance of movement for fish recaptured in month j which had moved in direction k and

r_{ijk} = distance of movement for fish recaptured in area i during month j which had moved in direction k,

$$V_{jk} = \frac{\sqrt{\left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \sin \Theta_k\right)^2 + \left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \cos \Theta_k\right)^2}}{\sum_{i}^{n_{jk}} \left(\frac{t_{ijk}}{f_{ij}}\right)} \tag{11}$$

where

V_{jk} = adjusted mean velocity of dislocation for fish recaptured in month j which had moved in direction k, and

$$A_{jk}^2 = \frac{1}{\sum_{i}^{n_{jk}} (1/f_{ij})} \left[\sum_{i}^{n_{jk}} \frac{r_{ijk}^2}{t_{ijk}\, f_{ij}} - \frac{\left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \sin \Theta_k\right)^2 + \left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \cos \Theta_k\right)^2}{\sum_{i}^{n_{jk}} \left(\frac{t_{ijk}}{f_{ij}}\right)} \right] \tag{12}$$

where

A_{jk}^2 = adjusted mean square dispersion coefficient for fish recaptured in month j which had moved in direction k.

The significance of the mean velocity of dislocation and the mean square dispersion coefficient has been discussed by Jones (1959 and 1966). Briefly, the former pertains to directional movement and the latter to random movement. The latter is a measure of the average amount of deviation from the mean direction of movement. A high value of $v_{j.}$ (or $V_{j.}$) and a low value of $a_{j.}$ or ($A_{j.}$) would indicate directional movement with little dispersion, while a low value of $v_{j.}$ (or $V_{j.}$) and a high value of $a_{j.}$ (or $A_{j.}$) would indicate the reverse. Even if the movement is entirely random, the values of $v_{j.}$ (or $V_{j.}$) would not be expected to equal 0 for most of the present groups of releases because they were made close to shore, and the fish were restricted in their movements toward shore.

The directions and average distances of movement, as calculated from the unadjusted return data, are shown on the left sides of Figure 5. The number in the center of the first diagram indicates the number of fish which did not move from the locations of release. (As explained by Schaefer, Chatwin, and Broadhead (1961), because of lack of precision in recording positions at sea, fish which moved 10 or 20 miles are often recorded as having been recaptured at the location of release.) The numbers near the heads of the arrows indicate the numbers of fish which moved in each direction and the average distances of movement, respectively. The widths of the circle and of the lines are proportional to the percentages of the fish which were recaptured in the locations of release and the percentages which moved in each direction. The lengths of the lines are proportional to the average distances of movement.

The fish released in the Acapulco area in 1960 were recaptured primarily to the northwest, while those released in the Manzanillo area in 1960 and in the Manzanillo and Acapulco areas in 1969 appear to have migrated mostly to the southeast. The fish released offshore were recaptured mainly to the east and northeast. The average distances of movement of the fish released in the Acapulco area in 1960 were less than those of the fish of the other groups of releases. It can be seen in Figure 4 that most of the former were recaptured shortly after release, whereas most of the latter were at liberty longer, so the mean velocities of dislocation are not necessarily less for the fish released in the Acapulco area in 1960.

Diagrams equivalent to those on the left sides of Figure 5 are shown on the right sides of that figure for the adjusted return data. The results are quite similar to those obtained for the unadjusted data. It appears that there was a considerable migration in Direction 6 from the 10°N-108°W area, but it can be seen on the left side of the figure that this is based upon only three returns, coupled with relatively little fishing effort in the corresponding 5-degree area-month strata.

The migrations appear to have been much more directed for the fish released in 1960 than for those released in 1969. To investigate this further the distributions of fishing effort and returns were plotted by 1-degree areas and months. These data showed more clearly than do those in Table 2 that there was relatively little effort to the southeast of the Acapulco area, and particularly to the northwest of the Manzanillo area, during the months when most of the tagged fish were recaptured. Thus there are two possibilities, (1) that the movement was strongly directed, which caused the effort to be distributed the way it was, or (2) that the distribution of the effort caused the movement to appear to be strongly directed, even though such was not the case. The former explanation is the more likely if the distributions of the tagged fish during the periods after release were about the same as those of most of the fish in the same general area and the weather permitted the vessels to fish where the fish were most concentrated. The latter explanation is more likely if the distribution of the fishing effort was the result of the distributions of fish other than those of the groups to which the tagged fish belonged or the result of weather conditions which caused the vessels to avoid some of the areas to which the tagged fish migrated. In general, the weather is poor between Acapulco and Manzanillo from about July through October, between Costa Rica and Manzanillo from about August through October, and in the Gulf of Tehuantepec from about November through March. The fishing effort has always been relatively low in the Gulf of Tehuantepec. The results of the 1969 experiments indicate that the movement was probably more nearly random for the fish of the 1960 experiments than the data indicate. This modifies the conclusion of Fink and Bayliff (1970), who on the basis of the results obtained with the Jones method with unadjusted data stated that the movements of the fish released in 1960 were strongly directed.

There is no provision in these diagrams for indicating the times at liberty or dates of recapture, and this could be done only by substituting several diagrams for each of the present ones.

The directions and average distances of movement by month of recapture, as calculated from the unadjusted return data, are shown on the left sides of Figure 6. The data for fish moving in different directions are shown in different panels within each graph. The points for consecutive months are joined by solid lines and those for non-consecutive months by dashed lines. The numbers near the points indicate the numbers of fish in each month. The values of $v_{\cdot k}$ appear in all the panels, and the values of $a_{\cdot\cdot}^2$ in the bottom panels. These diagrams are useful for detecting seasonal migrations. For instance, if the fish were at the southern end of their range in January and at the northern end of it in July, and they were tagged in January, $\overline{r_{j\cdot}}$ would increase for about 6 months and then decrease. Also, there would be many fish in the panels for Directions 0 and 7 and few in the panels for Directions 3 and 4 during February-June, whereas the reverse would be true during August-December. Seasonal migrations are not apparent, the distances from the locations of release tending only to stay constant or increase with time. The velocities in each direction were roughly the same for all the experiments, but the velocities in the bottom panels for the 1960 experiments were greater because most of the fish which were recaptured had moved in the same directions.

Diagrams equivalent to those on the left sides of Figure 6 are shown on the right sides of that figure for the adjusted return data. These diagrams appear quite similar to the corresponding ones for the unadjusted data, the principal differences being in the numbers of fish. One notable example appears in the Direction-6 panel for the fish released in the Acapulco area in 1969; in this case a single return for October was adjusted to 34 returns because the effort in the 5-degree area-month stratum of recapture was low. The differences in the directions of movement for the unadjusted and adjusted returns for February from the fish released in the Acapulco area in 1969 are of interest. For the unadjusted data, 7 of the recaptures were made to the southeast (Directions 2 and 3) and 36 to the northwest (Directions 6 and 7); for the adjusted data 24 of the recaptures were made to the southeast and 12 to the northwest. This indicates that the fish released in the Acapulco area in 1969 tended to be distributed more to the southeast than to the northwest (*i.e.* in or near the Manzanillo area) in February 1970.

The mean square dispersion coefficients by months of recapture, as calculated from the unadjusted return data, are shown on the left side of Figure 7. The points are plotted only for the months which include at least five returns. The numbers near the points indicate the numbers of returns in each month. The $a_{j\cdot}^2$ values are higher for the experiments initiated in 1969 because the effort was spread over a much greater area in 1970, which resulted in the recaptures also being spread over a much greater area. The trends are quite similar to those for the averages of the squared distances of movement (Figure 4). However, there is no tendency for the $a_{j\cdot}^2$ values to increase with time, except possibly for the fish released in the Acapulco area in 1969. The $a_{j\cdot}^2$ values for February are low for the fish released in the Manzanillo area in 1969 and high for the fish released in the Acapulco and 10°N-100°W areas in that year, this probably being due to the large amount of fishing effort exerted in the Manzanillo area and the low amount exerted in the Acapulco area in February 1970.

Diagrams equivalent to those on the left side of Figure 7 area shown on the right side of that figure for the adjusted return data. The results are quite similar to those obtained for the unadjusted data, the principal difference being that there does not appear to be an increasing trend for the fish released in the Acapulco area in 1969. For the reason given in the discussion of the Skellam method, it is logical to assume that the high effort exerted in the Manzanillo area during 1970 was due at least partly to an influx of fish from the Acapulco and 10°N-100°W areas.

Variance-covariance method

With this method Cartesian coordinates, instead of the polar coordinates used in the Jones method, are employed. Each fish is assumed to have been released at point (0,0), and the location of recapture is expressed as distances east or west (X) and north or south (Y) of that point. The variance-covariance matrix for the recaptures in month j from a group of releases is calculated by

$$\begin{bmatrix} \sum^{n_j} (X_j - \overline{X}_j)^2/n_j - 1 & \sum^{n_j} (X_j - \overline{X}_j)\ (Y_j - \overline{Y}_j)/n_j - 1 \\ \sum^{n_j} (X_j - \overline{X}_j)\ (Y_j - \overline{Y}_j)/n_j - 1 & \sum^{n_j} (Y_j - \overline{Y}_j)^2/n_j - 1 \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \tag{13}$$

where

n_j = number of returns during month j,

$\overline{X}_j = \sum^{n_j} X_j/n_j$, and

$\overline{Y}_j = \sum^{n_j} Y_j/n_j$.

The determinant of the variance-covariance is calculated by

$$(a_{11} \times a_{22}) - (a_{12} \times a_{21}) \tag{14}$$

and the coefficient of correlation by

$$[(a_{12} \times a_{21})/(a_{11} \times a_{22})]^{1/2} \ . \tag{15}$$

It is apparent that if the movement of the group of fish was approximately at a 45-degree angle to the abscissa and ordinate, *viz* northeast, southeast, southwest, or northwest (or in two opposite directions), the correlation coefficient would be more likely to be significant than if it was approximately along one of the axes, *viz* north and/or south or east and/or west. To remedy this bias the axes were rotated, employing a method devised by Dr. Robert C. Francis. The transformed abscissa and ordinate were those axes through the origin which were at 45-degree angles to the direction of maximum variability in the original Cartesian coordinate system. That direction was determined by computing the first eigenvector of the original variance-covariance matrix. This procedure maximizes the correlation coefficients.

The adjusted variance-covariance matrix is calculated by

$$\begin{bmatrix} \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij}-\overline{X}_{ij})^2/n_j-1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) & \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij}-\overline{X}_{ij})\ (Y_{ij}-\overline{Y}_{ij})/n_j-1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \\ \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij}-\overline{X}_{ij})\ (Y_{ij}-\overline{Y}_{ij})/n_j-1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) & \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (Y_{ij}-\overline{Y}_{ij})^2/n_j-1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \end{bmatrix} \tag{16}$$

where

$$\overline{X}_{ij} = \sum_{i}^{n_j} (X_{ij}/f_{ij}) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \quad \text{and}$$

$$\overline{Y}_{ij} = \sum_{i}^{n_j} (Y_{ij}/f_{ij}) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \ .$$

The determinant of the variance-covariance matrix and the correlation coefficient are obviously closely related since the first is obtained by subtracting a smaller number from a larger one and the second is obtained by dividing the same smaller number by the same larger one and then taking the square root of the quotient. The determinant of the variance-covariance matrix is an index of the dispersion of the fish; when the distances of the fish from one another are large the determinant is large. Thus it is very similar to $a_{j\cdot}^2$ of the Jones method. The correlation coefficient approaches 0 when the movement is random and approaches 1 when most of the movement is in only one direction or in two opposite directions.

The variance-covariance method is based on probabilities, so when the data are adjusted this invalidates the estimates of the determinant of the variance-covariance matrix and the correlation coefficient. Nevertheless, these estimates are shown in the figures for comparison with those obtained with the unadjusted data.

The average locations of recapture by months of recapture, as calculated from the unadjusted return data, are shown on the left sides of Figure 8. The points are plotted only for the months which include at least five returns. The numbers near the points indicate the months of recapture (1 = January, 2 = February, etc.). Again it is apparent that the fish released in the Acapulco area in 1960 were recaptured mostly to the northwest and that those released in the Manzanillo area in that year were recaptured mostly to the southeast. It is also again apparent that the fish released in the Manzanillo and Acapulco areas in 1969 were recaptured mostly to the southeast, while those released offshore were recaptured mostly to the east and northeast. However, the fish released in the Acapulco area in 1969 appeared mostly to the northwest of the area of release in February 1970, coincident with the large amount of fishing effort in the Manzanillo area during that month. Likewise, the fish released in the 10°N-100°W and 10°N-108°W areas in 1969 appeared more to the north of the area of release in February than in the other months of 1970.

Diagrams equivalent to those on the left sides of Figure 8 are shown on the right sides of that figure for the adjusted return data. The diagrams on the left and right sides of this figure differ more from one another than do those on the left and right sides of any other figure. It appears that the fish released in the Acapulco area in 1969 did not migrate in large numbers to the Manzanillo area near the beginning of February 1970; thus the total catch was large in that area during that month because the fish which were already there became more vulnerable to the fishery or because there was an ingress of fish of groups other than those to which the fish released in the Acapulco area in 1969 belonged. The same applies to the fish released at 10°N-100°W in 1969; their movement near the beginning of February 1970 was primarily to the east.

The unadjusted and adjusted determinants of the variance-covariance matrices by months of recapture are shown on the left and right sides of Figure 9. The results are similar to those shown in Figures 4 and 7, the principal difference being that the differences among the six groups of releases are greater for the ranges of the determinants than for the ranges of the parameters in the other two figures. The results were expected to be especially similar to those in Figure 7, but they indicate an increasing trend with time for the fish released in the Acapulco area in 1969, which is more similar to the trend in Figure 4 than to that in Figure 7.

The unadjusted and adjusted correlation coefficients by months of recapture are shown on the left and right sides of Figure 10. The results are similar to those shown in Figures 4, 7, and 9, particularly Figure 7. Only two unadjusted correlation coefficients for months with more than six returns were not significant at the 5-percent level; these were the correlation coefficients for the Manzanillo area for January 1970 (d. f. = 17, $r = 0.217$) and the 10°N-100°W area for January 1970 (d. f. = 27, $r = 0.356$). For both of these the adjusted correlation coefficients were significant, however ($r = 0.669$, $P < 0.01$ for the former and $r = 0.649$, $P < 0.01$ for the latter). For the adjusted data there was only one non-significant correlation coefficient for a month with more than six returns; in this case it was for the Acapulco area for March 1970 (d. f. = 67, $r = 0.217$).

Lengths of the fish and effect of length on direction of movement

It is desirable to compare the distributions of the lengths at the times of release of the tagged fish which were returned to the length-frequency distributions of fish caught in the same areas at the same times to see if the former were representative of the latter. Also, it is desirable to compare the directions of movement of fish of different lengths.

Data on the length-frequency distributions of fish in the catches are obtained routinely from measurements of samples of 50 fish shortly after they are unloaded from the vessels at the canneries (Hennemuth, 1957). The pertinent data are shown in Figure 11. The length-frequency data for the Acapulco area in 1960 consist of nine samples of fish caught by baitboats in that area in March and April 1960. Those for the Manzanillo area in 1960 consist of one sample of fish caught by a baitboat in that area in August 1960; these data are not shown in the figure because the tagged fish released in August 1960 were not measured. The length-frequency data for 1969 consist of one sample of fish landed by the vessel which was used for tagging. (No other samples were obtained because, due to the regulation mentioned previously, there were no other vessels fishing in the area during the last quarter of 1969.) This sample included a mixture of fish caught in Acapulco and 10°N-108°W areas. It was biased because fish were removed from those caught for tagging and, as will be shown below, equal portions of fish of all sizes caught were not selected for this purpose.

Data on the distributions of the lengths at the times of release of the tagged fish which were returned are also shown in Figure 11.

The catch in the Acapulco area in 1960 appears to have consisted of three groups of fish, while almost all of the tagged fish which were returned appear to have belonged to the middle group. Thus the data presented in this report may be representative only of the migrations of the fish of the middle group.

The fish tagged in the Manzanillo area in 1960 were probably about 50-60 cm long (Fink and Bayliff, 1970: 57). The 50 fish of the corresponding sample of the catch were mostly 54 to 62 cm long, so the tagged fish were probably fairly representative of those caught in that area during that month.

The biased sample of the catch in the Acapulco and 10°N-108°W areas in 1969 indicates two groups of fish, one including fish less than 100 cm long and the other including fish more than 110 cm long. The great majority of the tagged fish which were returned were less than 100 cm long at the times of release. Thus in this case the data presented in this report may be representative only of the migrations of the smaller fish.

The fish of the largest group, those released in the Acapulco area in

1969, were selected for comparison of the directions of movement of fish of different lengths. A graph of the frequencies of the lengths of the tagged fish released in this area was prepared, and on the basis of this the fish which were returned were divided into the following categories: small 42-71 cm (62 fish); medium, 72-93 cm (294 fish); large, 94-126 cm (18 fish) ; unknown (5 fish). A preliminary examination of the data indicated that the small fish tended to migrate more to the northwest than to the southeast, whereas the reverse was true for the medium and large fish. It was observed that the portions of small and medium fish differed among sets made in different locations in the Acapulco area, so the differences in direction of movement might be due to the differences in location of release rather than to differences in length of the fish. To examine this the data were divided into five locations of release, three directions of movement, southeast (Directions 2 and 3), southwest (Directions 4 and 5), and northwest (Directions 6 and 7), and two lengths, small and medium. Fish had been released in seven 1-degree areas, but the data for two of them were combined with those of the nearest two 1-degree areas to avoid empty cells. The data for fish which moved in Directions 0 and 1 and those for large fish were not considered because there were so few in those categories. The results of *G* tests (Sokal and Rohlf, 1969: 601-607) are as follows:

Hypothesis	**Degrees of freedom**	***G***	**Probability**
Location × length independence	4	34.046	< 0.01
Location × direction independence	8	33.056	< 0.01
Length × direction independence	2	20.936	< 0.01
Location × length × direction interaction	8	2.798	> 0.05
Total	22	91.286	

The non-significance of the interaction indicates either that the difference in directions of movement of the small and medium fish was caused by differences in the portions of small and medium fish released in the different locations or that the difference in directions of movement of the fish released in the different locations was caused by differences in the portions of small and medium fish in those locations. Examination of the data reveals that the latter is the case; thus the small fish tended to migrate more to the northwest and the medium fish more to the southeast.

A Chi-square contingency test indicated no difference in the directions of movement for the medium and large fish ($\chi^2 = 0.533$, d.f. $= 2$, $P > 0.05$). However, the number of large fish returned was limited, and most of these were smaller than the large fish of the sample (Figure 11). If equal portions of the catch of fish of all sizes had been tagged and returned there would probably have been more movement to the southeast and less to the northwest, but this is not certain because so few tagged fish larger than 100 cm were released.

SUMMARY AND CONCLUSIONS

The map method, the Jones method, and the variance-covariance method are all useful for studying the migrations of yellowfin, and each presents information which is complementary to that presented by the others. The Skellam method, as used in this report, is less useful.

The movements of the tagged fish released in 1960 appeared to have been strongly directed, but it was shown that this was probably caused principally by the distribution of the fishing effort. The effort was much more widely distributed in 1970, and the movement of the fish appeared to have been much less directed. The correlation coefficients derived from the variance-covariance method showed that it was by no means random, however.

One of the most interesting questions is whether or not a major portion of the tagged fish released in the Acapulco and 10°N-100°W areas in 1969 migrated northwest to the Manzanillo area near the beginning of February 1970. If the data had been analyzed only by the Skellam method it would have been concluded that such was the case. However, employment of the map, Jones, and variance-covariance methods showed that when the data are adjusted the movement to the Manzanillo area was relatively unimportant. An analysis of the movement by length indicated that the small fish tended to move to the northwest and the medium and large fish tended to move to the southeast.

It would be desirable to compare data on tagged fish released in the same areas during the same months in other years to determine the extent of variation in the migrations in different years. Such experiments were initiated on a smaller scale in 1970, 1971, 1972, and 1973, and such comparisons will eventually be made. It would also be desirable to study the migrations of tagged fish released in other areas, particularly off Central America and outside the CYRA. Tagged fish were released in these areas in 1970 and 1971, but on a much smaller scale than necessary. The experiments off Central America were initiated during April, May, and June, but they should also be initiated during October, November, or December to take advantage of the peak period of fishing in that area during January through May. Finally, it would be desirable to tag and release more large fish. Unfortunately, however, these fish are so difficult to handle that this would be almost impossible to do.

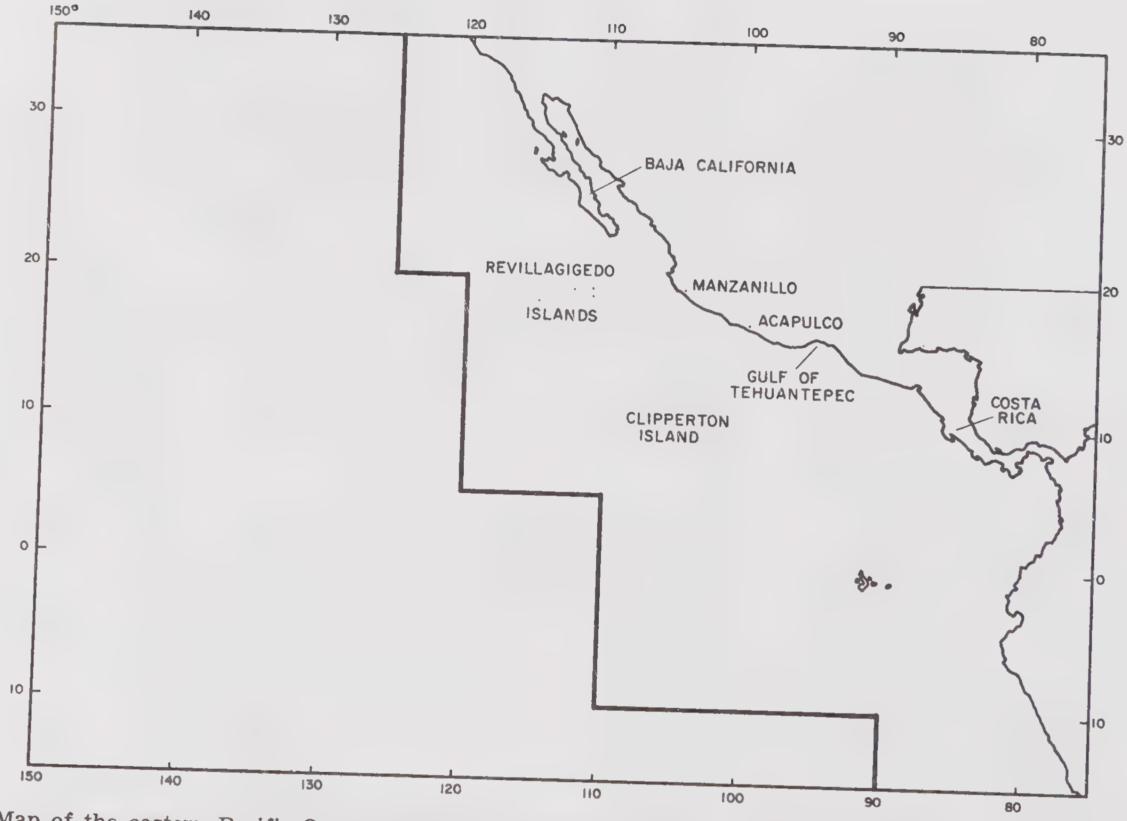

150°
140
130
120
110
100
90
80
30
20
10
0
10
150
BAJA CALIFORNIA
REVILLAGIGEDO ISLANDS
MANZANILLO
ACAPULCO
GULF OF TEHUANTEPEC
CLIPPERTON ISLAND
COSTA RICA

FIGURE 1. Map of the eastern Pacific Ocean, showing the areas mentioned in the text. The heavy line is the boundary of the Commission's yellowfin regulatory area.

FIGURA 1. Mapa del Océano Pacífico oriental, en el que se indican las áreas mencionadas en el texto. La línea gruesa es el límite del área reglamentaria de la Comisión de aleta amarilla.

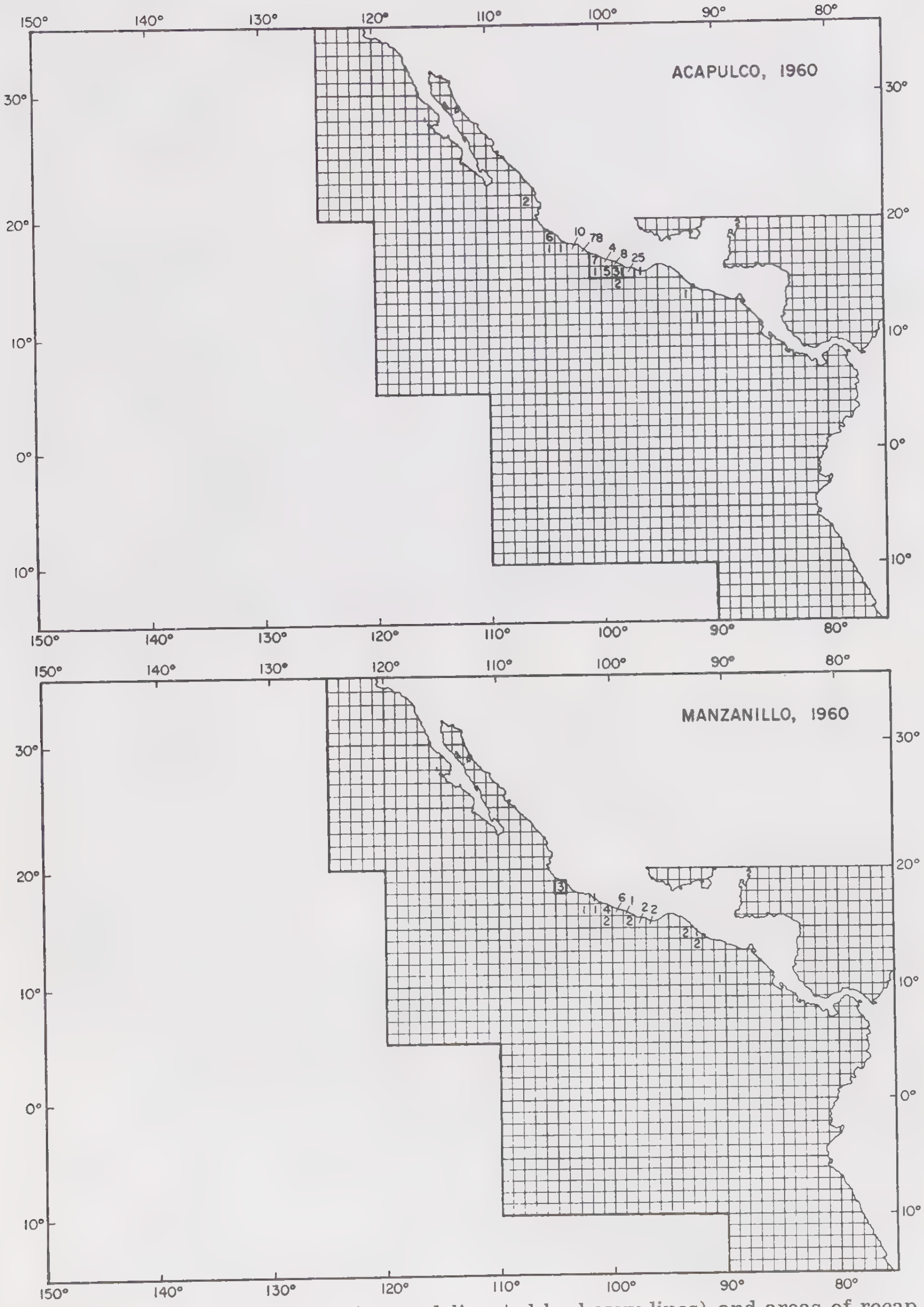

ACAPULCO, 1960
MANZANILLO, 1960
150°
140°
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°
10°

FIGURE 2. Areas of release (areas delineated by heavy lines) and areas of recapture (areas with numerals) for fish released off the southern coast of Mexico in 1960 and 1969.

FIGURA 2. Areas de liberación (áreas delineadas por líneas gruesas) y áreas de recaptura (áreas con cifras) de peces liberados frente a la costa meridional de México en 1960 y 1969.

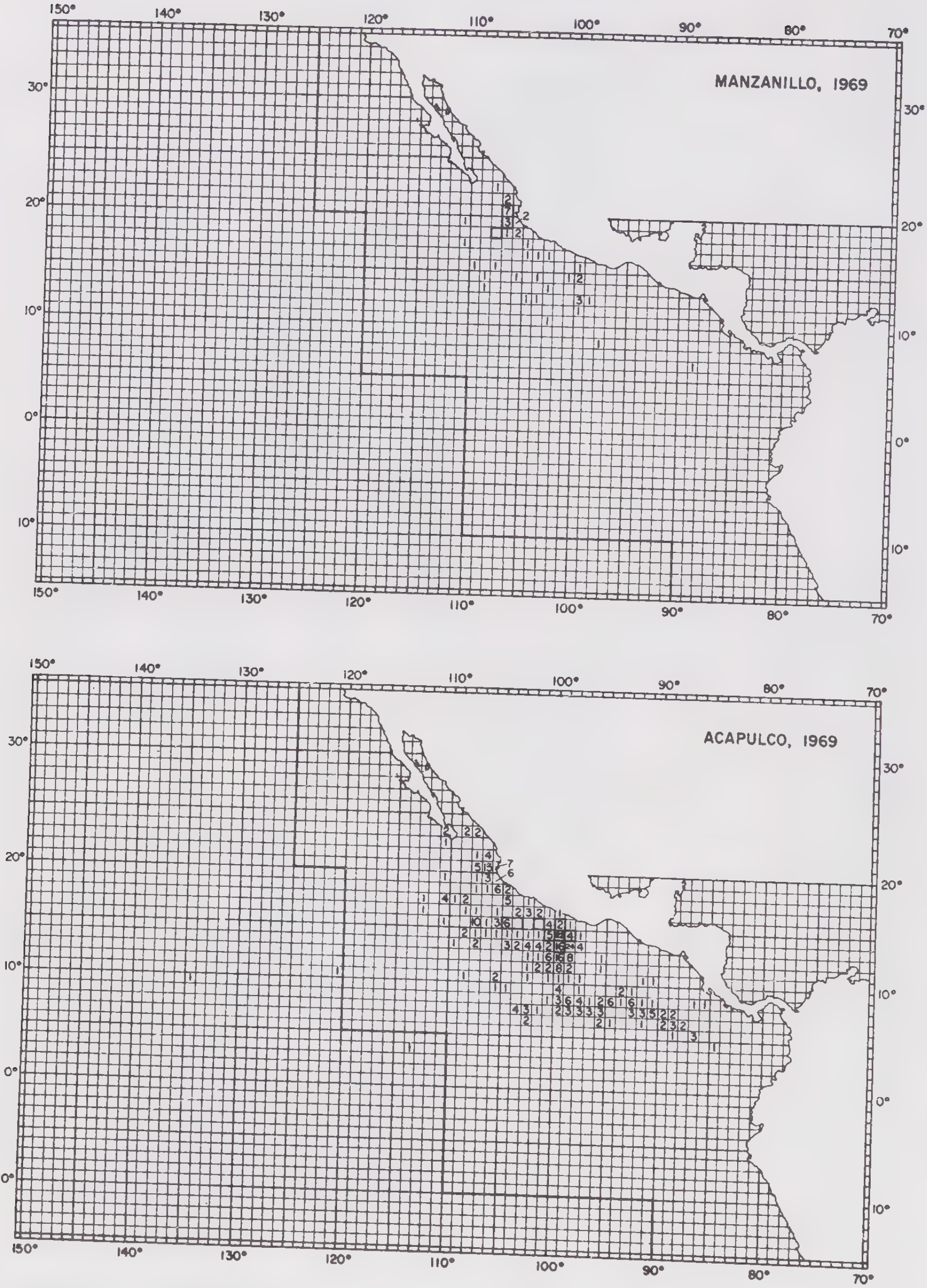
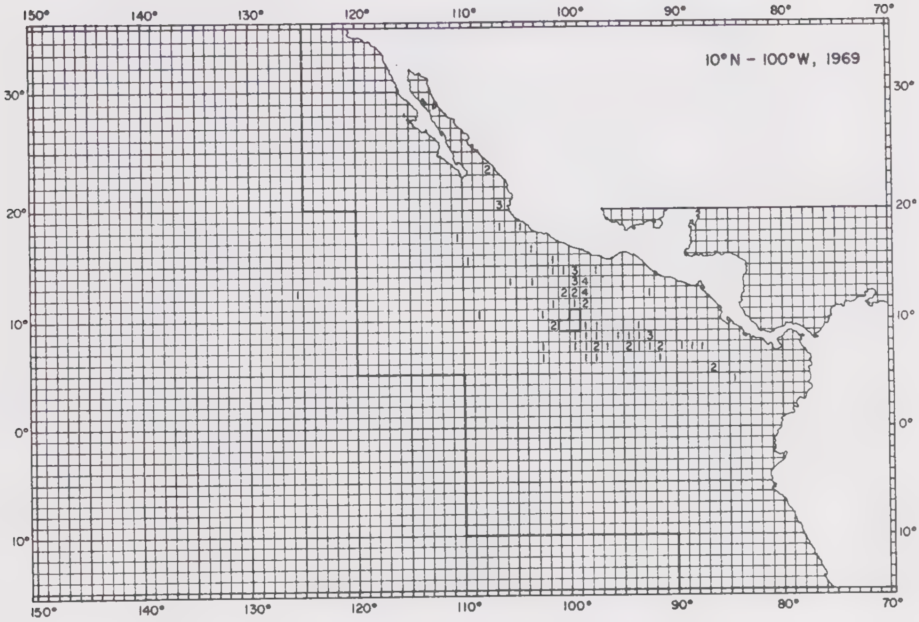

MANZANILLO, 1969
ACAPULCO, 1969
150°
140°
130°
120°
110°
100°
90°
80°
70°
30°
20°
10°
0°
10°

FIGURE 2. (Continued)

FIGURA 2. (Continuación)


10°N - 100°W, 1969
150°
140°
130°
120°
110°
100°
90°
80°
70°
30°
20°
10°
0°
10°

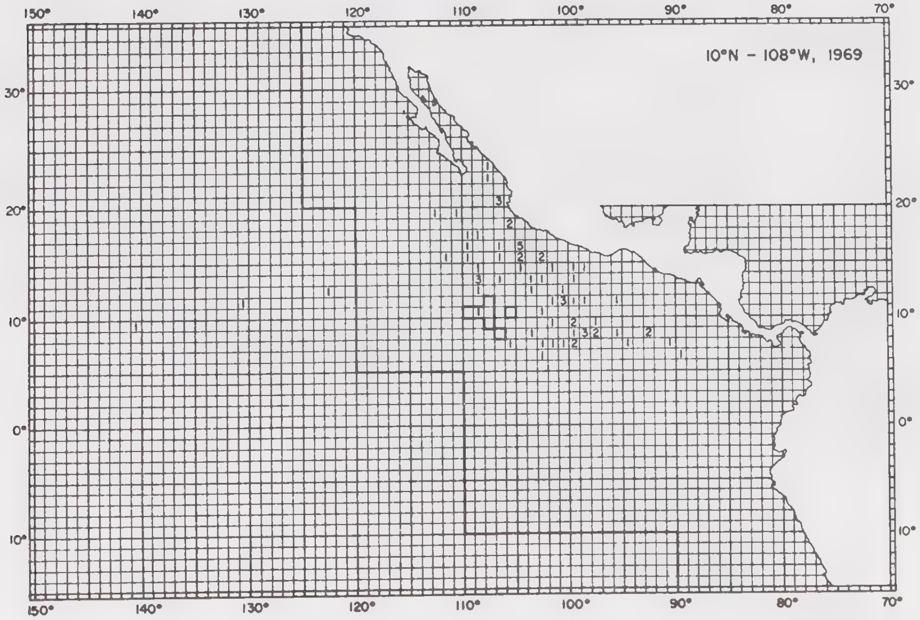

10°N - 108°W, 1969
150°
140°
130°
120°
110°
100°
90°
80°
70°
30°
20°
10°
0°
10°

FIGURE 2. (Continued)
FIGURA 2. (Continuación)

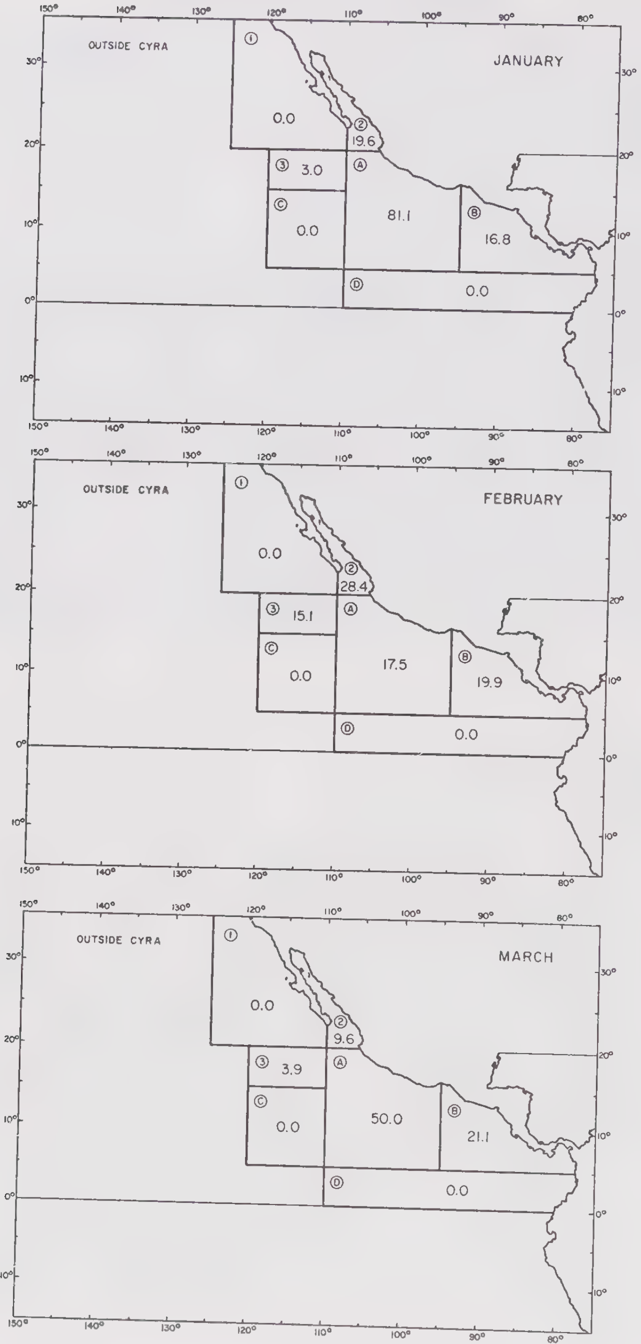

OUTSIDE CYRA
JANUARY
① 0.0
② 19.6
③ 3.0
Ⓐ 81.1
Ⓑ 16.8
Ⓒ 0.0
Ⓓ 0.0
OUTSIDE CYRA
FEBRUARY
① 0.0
② 28.4
③ 15.1
Ⓐ 17.5
Ⓑ 19.9
Ⓒ 0.0
Ⓓ 0.0
OUTSIDE CYRA
MARCH
① 0.0
② 9.6
③ 3.9
Ⓐ 50.0
Ⓑ 21.1
Ⓒ 0.0
Ⓓ 0.0
150°
140°
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°
10°

FIGURE 3. Adjusted tag returns during January-June 1970 of fish released off the southern Mexico coast during October-November 1969.

FIGURA 3. Devoluciones ajustadas de marcas durante enero-junio 1970 de peces liberados frente a la costa meridional de México durante octubre-noviembre 1969.

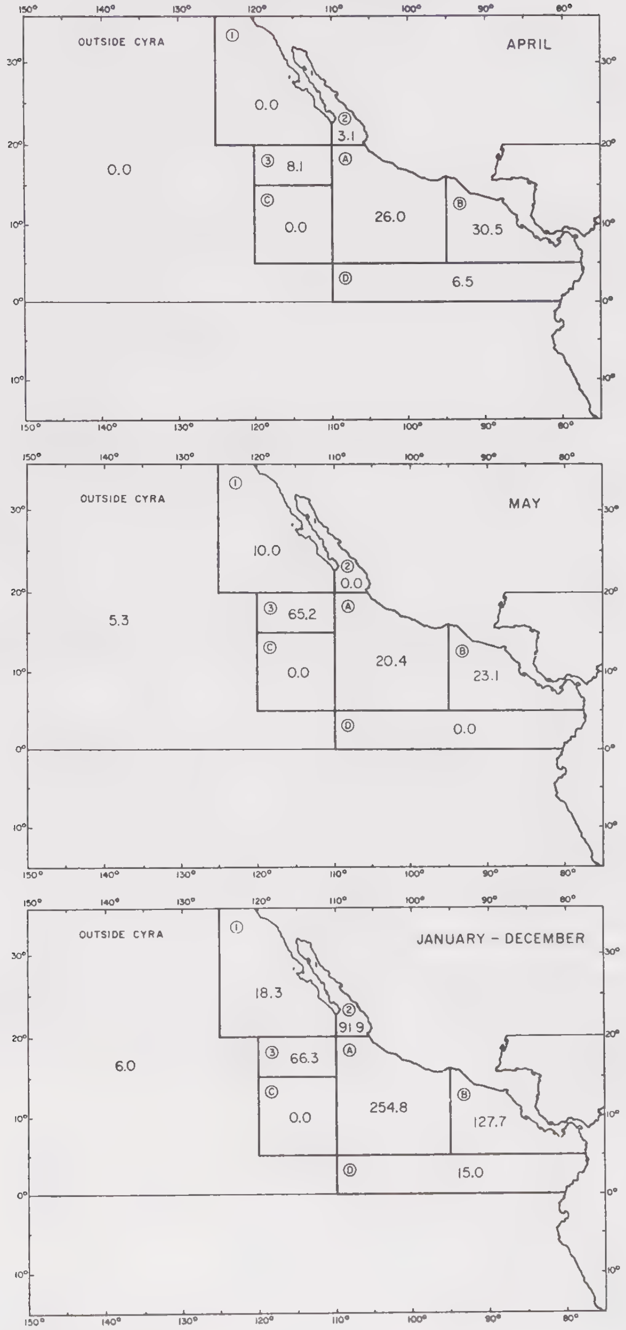

150° 140° 130° 120° 110° 100° 90° 80°
30° 20° 10° 0° 10°
APRIL
OUTSIDE CYRA
0.0
① 0.0
② 3.1
③ 8.1
Ⓐ 26.0
Ⓑ 30.5
Ⓒ 0.0
Ⓓ 6.5
MAY
OUTSIDE CYRA
5.3
① 10.0
② 0.0
③ 65.2
Ⓐ 20.4
Ⓑ 23.1
Ⓒ 0.0
Ⓓ 0.0
JANUARY – DECEMBER
OUTSIDE CYRA
6.0
① 18.3
② 91.9
③ 66.3
Ⓐ 254.8
Ⓑ 127.7
Ⓒ 0.0
Ⓓ 15.0

FIGURE 3. (Continued)
FIGURA 3. (Continuación)

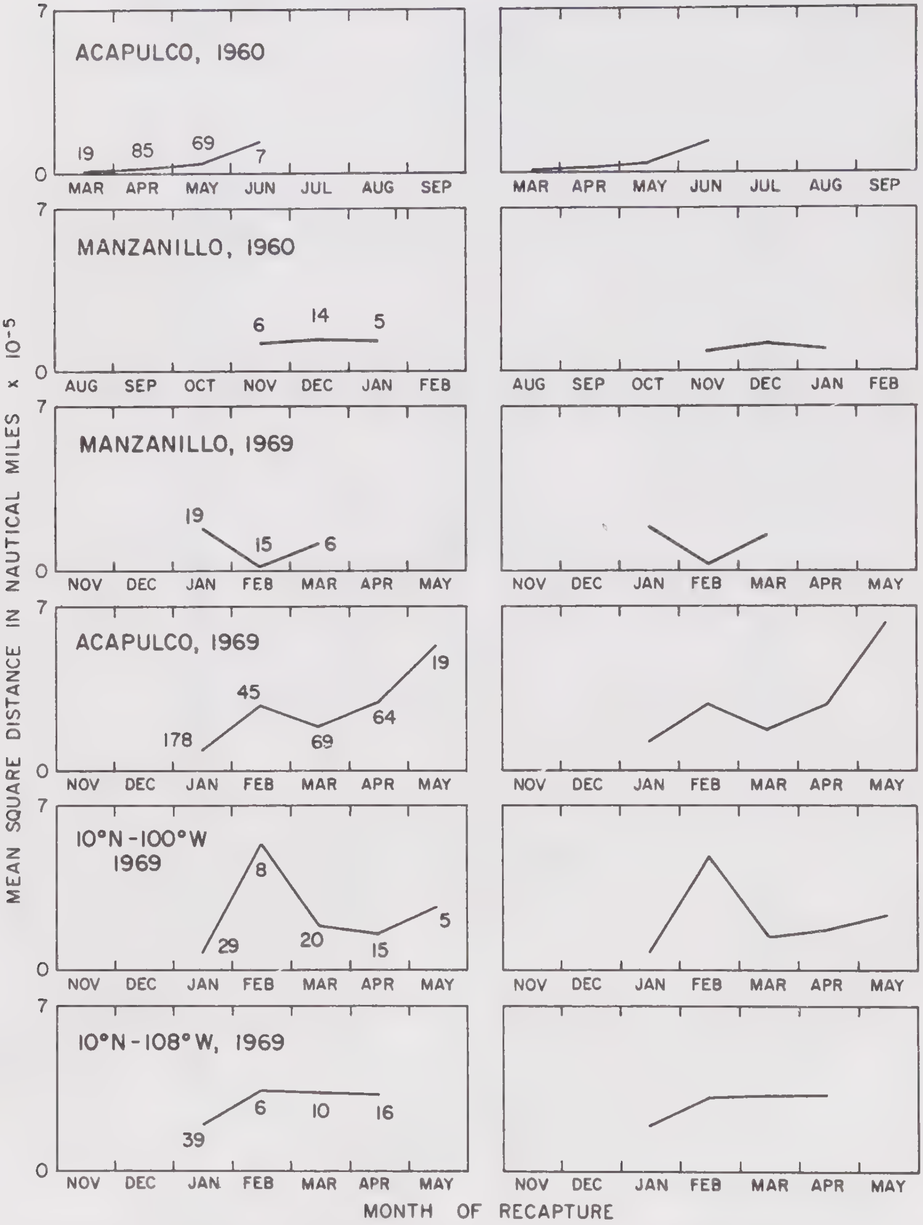


FIGURE 4. Unadjusted (left side of figure) and adjusted (right side of figure) averages of the squared distances of movement in nautical miles, by months of recapture.

FIGURA 4. Promedios sin ajustar (margen izquierdo de la figura) y ajustados (margen derecho de la figura) de las distancias cuadradas de desplazamiento en millas náuticas, por meses de recaptura.

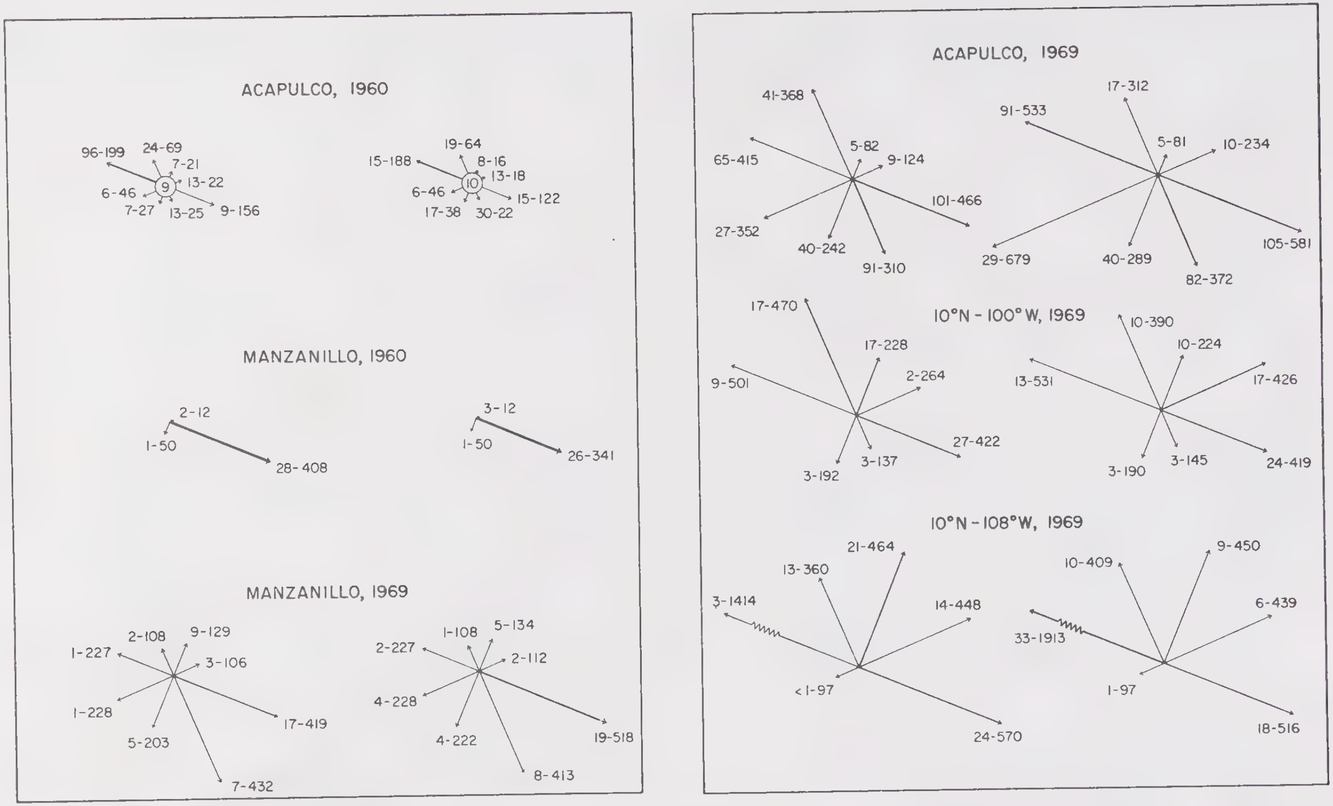

ACAPULCO, 1960
96-199
24-69
7-21
13-22
9
6-46
7-27
13-25
9-156
19-64
15-188
8-16
13-18
10
6-46
15-122
17-38
30-22
MANZANILLO, 1960
2-12
1-50
28-408
3-12
1-50
26-341
MANZANILLO, 1969
2-108
9-129
1-227
3-106
1-228
17-419
5-203
7-432
1-108
5-134
2-227
2-112
4-228
4-222
19-518
8-413
ACAPULCO, 1969
41-368
65-415
5-82
9-124
101-466
27-352
40-242
91-310
17-312
91-533
5-81
10-234
29-679
40-289
105-581
82-372
10°N - 100°W, 1969
17-470
17-228
9-501
2-264
27-422
3-192
3-137
10-390
10-224
13-531
17-426
3-190
3-145
24-419
10°N - 108°W, 1969
21-464
13-360
3-1414
14-448
<1-97
24-570
10-409
9-450
6-439
33-1913
1-97
18-516

FIGURE 5. Unadjusted (left sides of figure) and adjusted (right sides of figure) directions and mean distances of movement. The diagrams are explained in the text.

FIGURA 5. Direcciones y promedios de las distancias de desplazamiento sin ajustar (margen izquierdo de la figura) y ajustadas (margen derecho de la figura). Los diagramas se encuentran explicados en el texto.

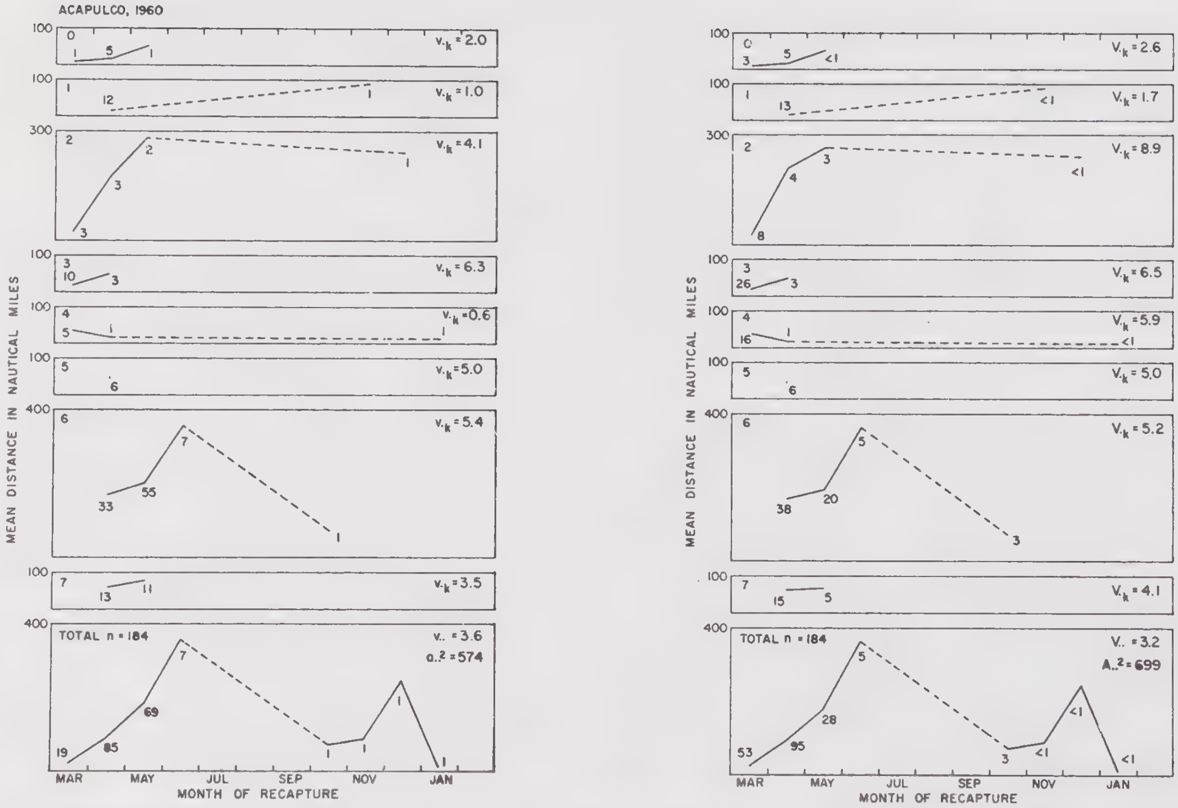


FIGURE 6. Unadjusted (left sides of figure) and adjusted (right sides of figure) dispersion, by months of recapture. The numbers in the upper left corners of the panels indicate the directions of movement.

FIGURA 6. Dispersión sin ajustar (margen izquierdo de la figura) y ajustada (margen derecho de la figura), por meses de recaptura. Las cifras en la esquina superior izquierda de los recuadros indican la dirección del desplazamiento.

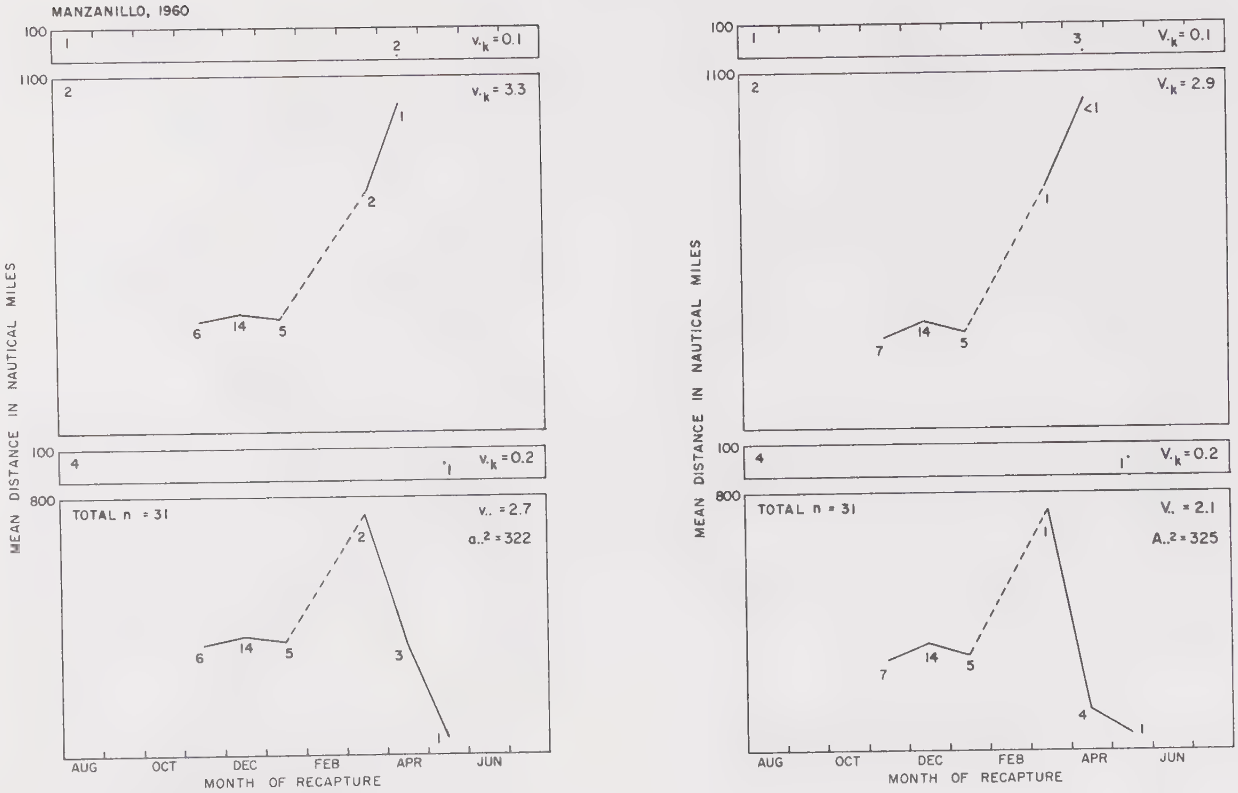


FIGURE 6. (Continued)

FIGURA 6. (Continuación)

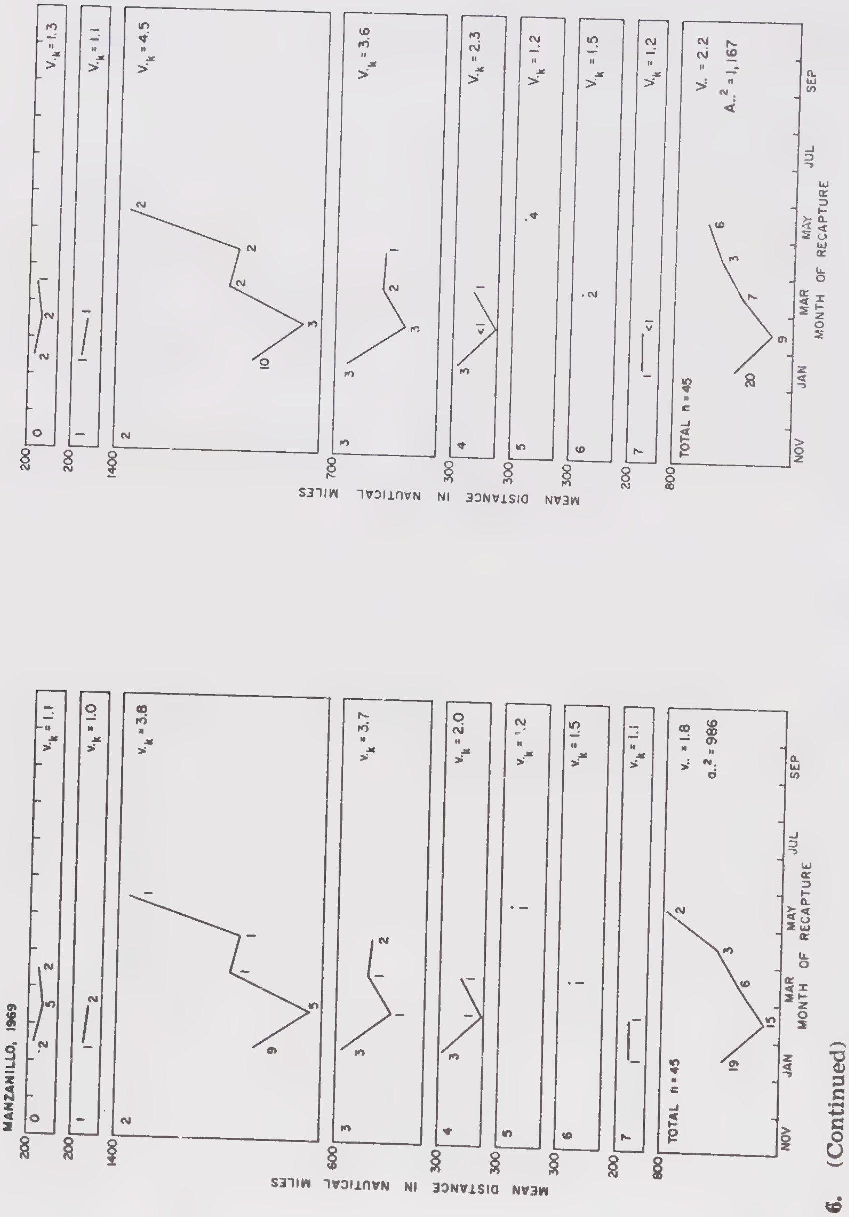


FIGURE 6. (Continued)

FIGURA 6. (Continuación)

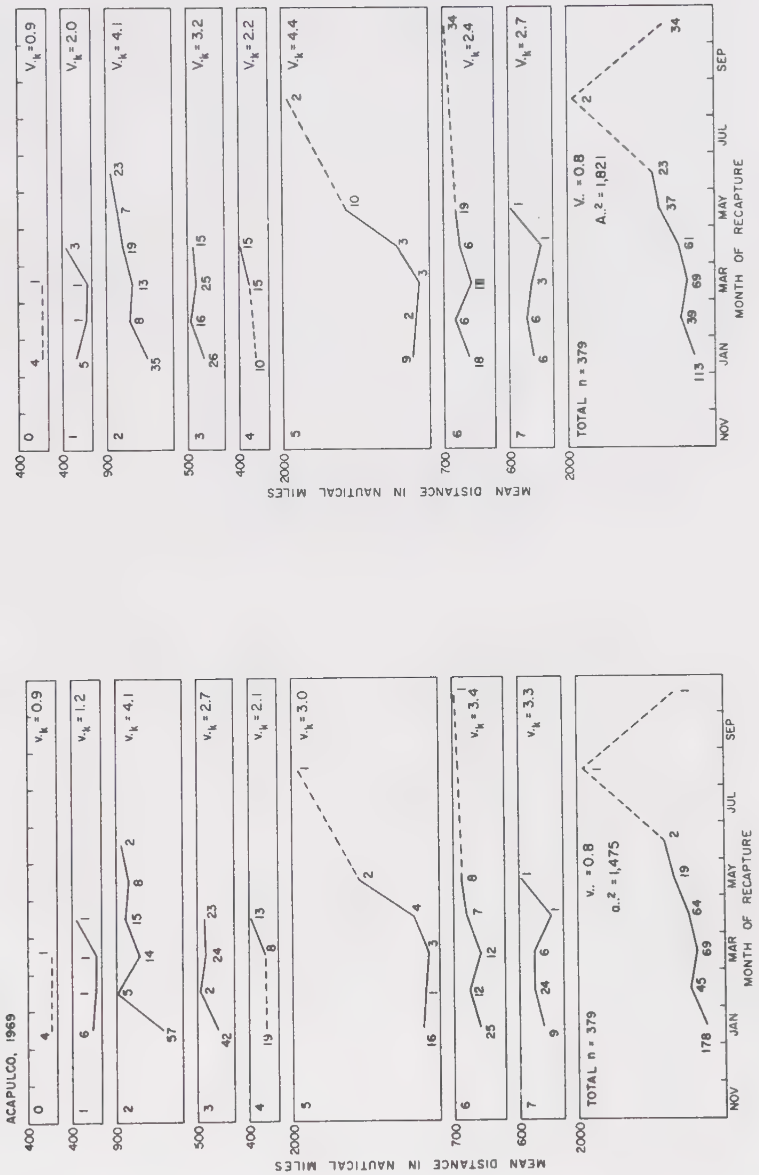


FIGURE 6. (Continued)
FIGURA 6. (Continuación)

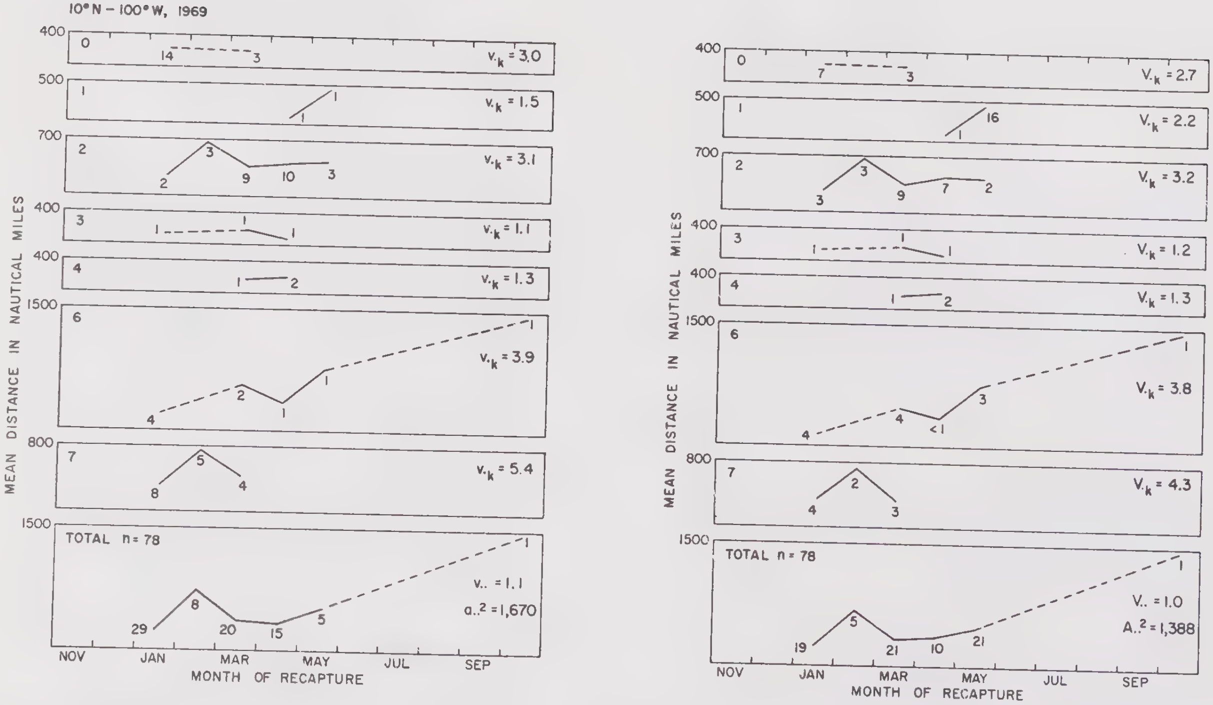


FIGURE 6. (Continued)

FIGURA 6. (Continuación)

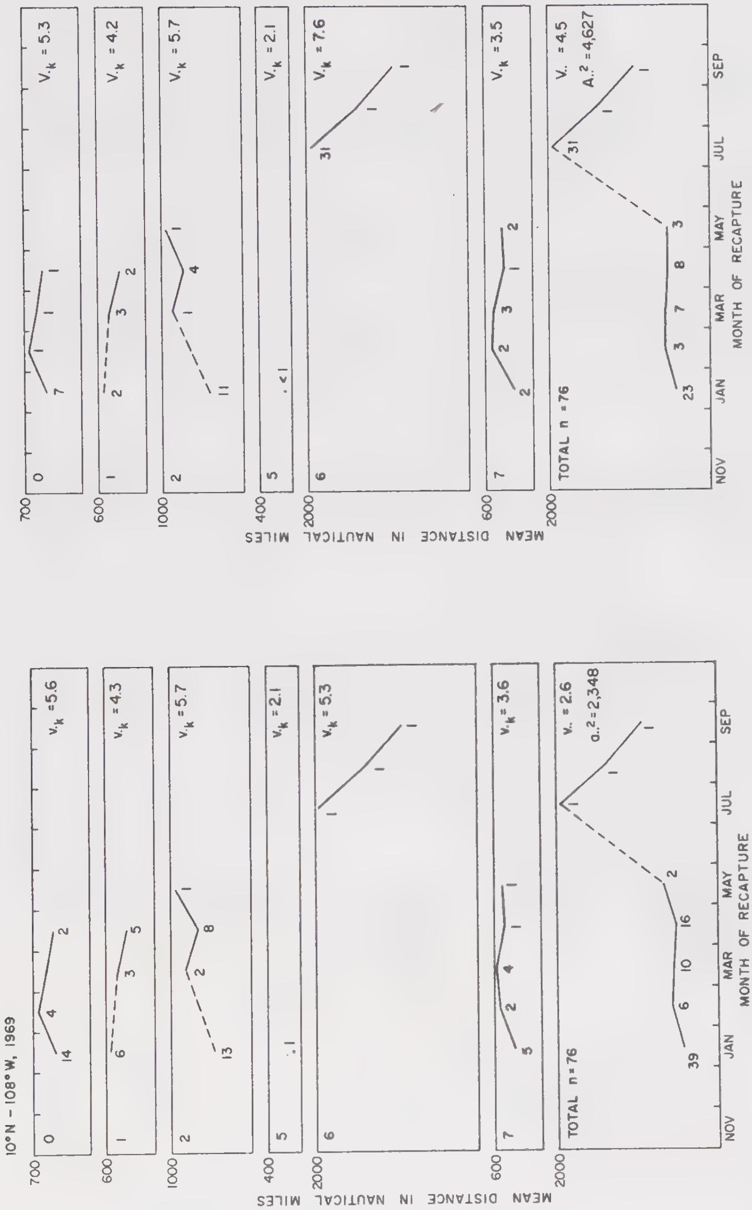


FIGURE 6. (Continued)

FIGURA 6. (Continuación)

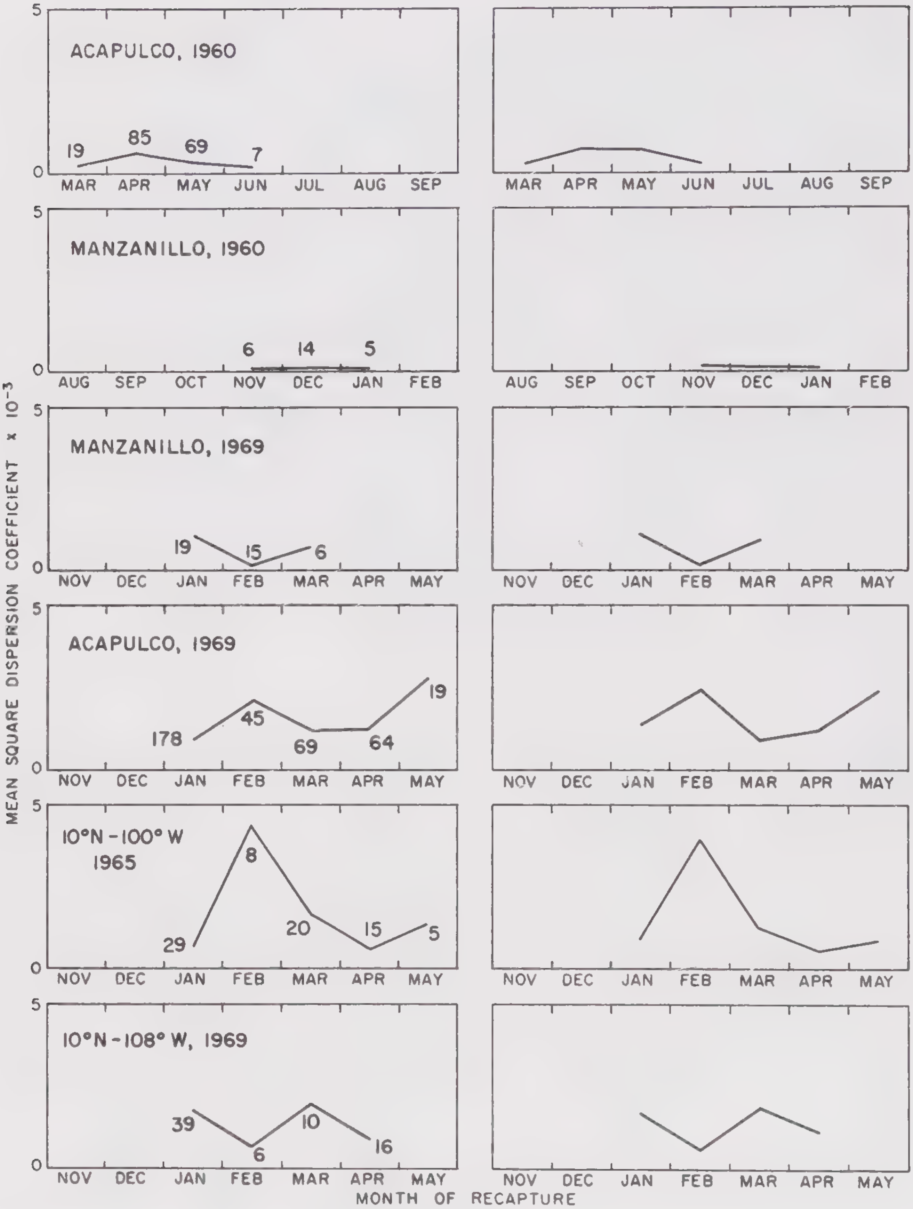


FIGURE 7. Unadjusted (left side of figure) and adjusted (right side of figure) mean square dispersion coefficients, by months of recapture.

FIGURA 7. Medias cuadradas del coeficiente de dispersión sin ajustar (margen izquierdo de la figura) y ajustada (margen derecho de la figura), por meses de recaptura.

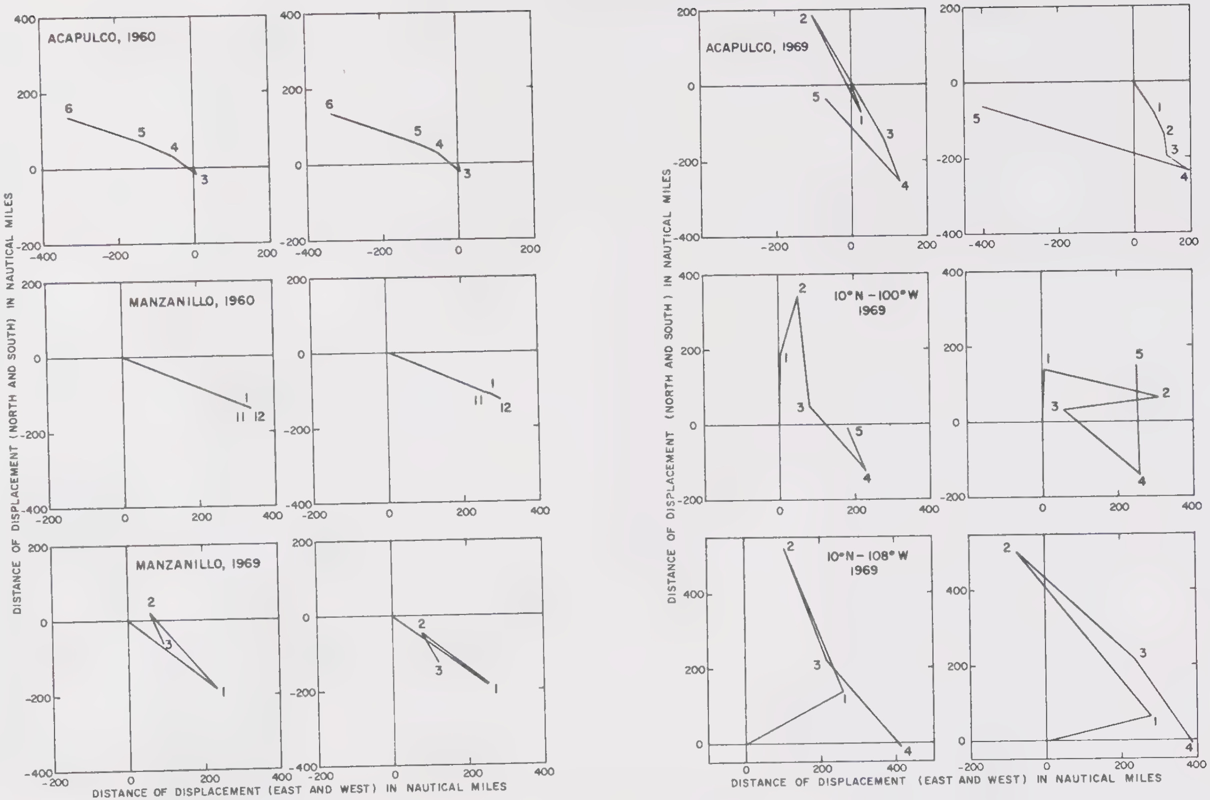


FIGURE 8. Unadjusted (left sides of figure) and adjusted (right sides of figure) average locations of recapture, by months of recapture.

FIGURA 8. Promedios de las localidades de recaptura sin ajustar (margen izquierdo de la figura) y ajustado (margen derecho de la figura), por meses de recaptura.

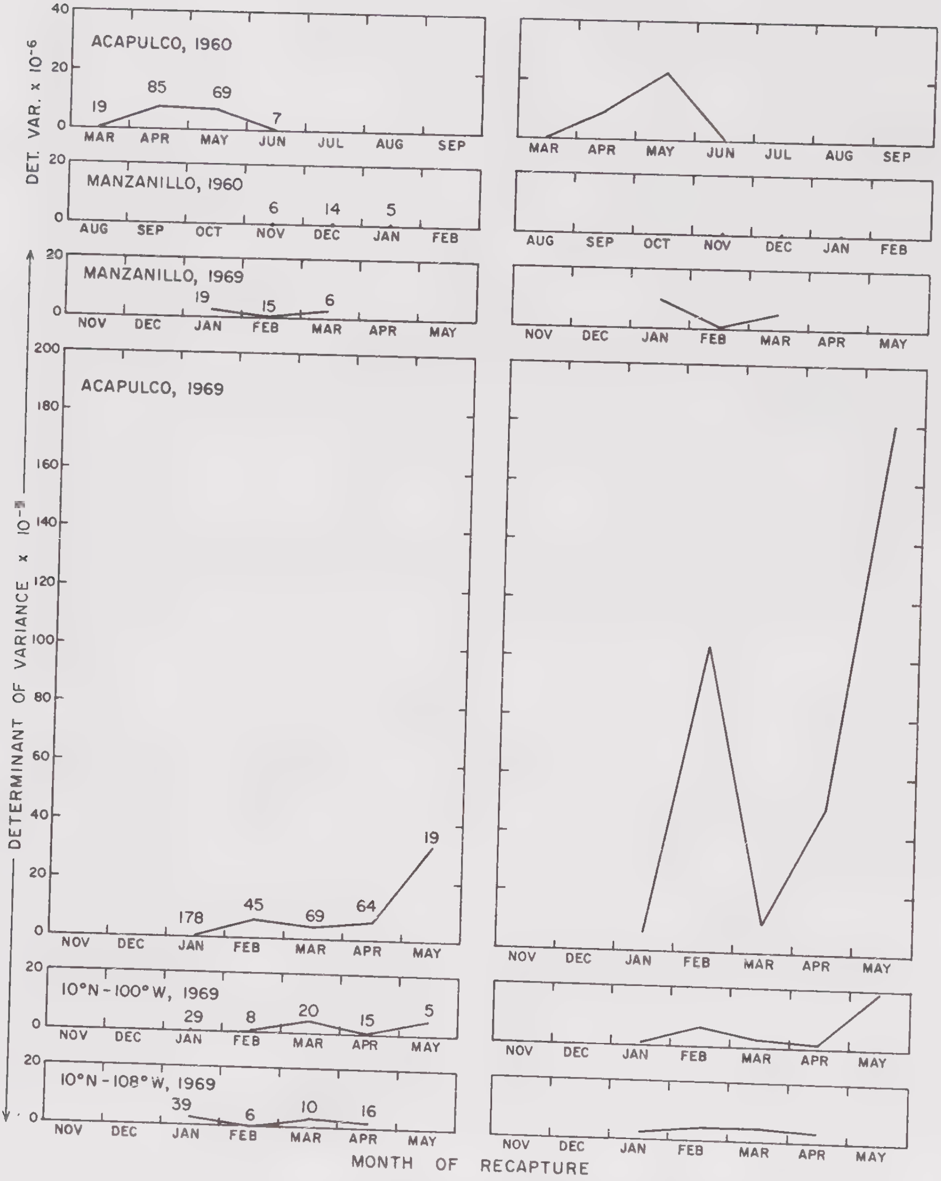


FIGURE 9. Unadjusted (left side of figure) and adjusted (right side of figure) determinants of variance-covariance matrices, by months of recapture.

FIGURA 9. Determinantes de las matrices variancia-covariancia sin ajustar (margen izquierdo de la figura) y ajustados (margen derecho de la figura), por meses de recaptura.

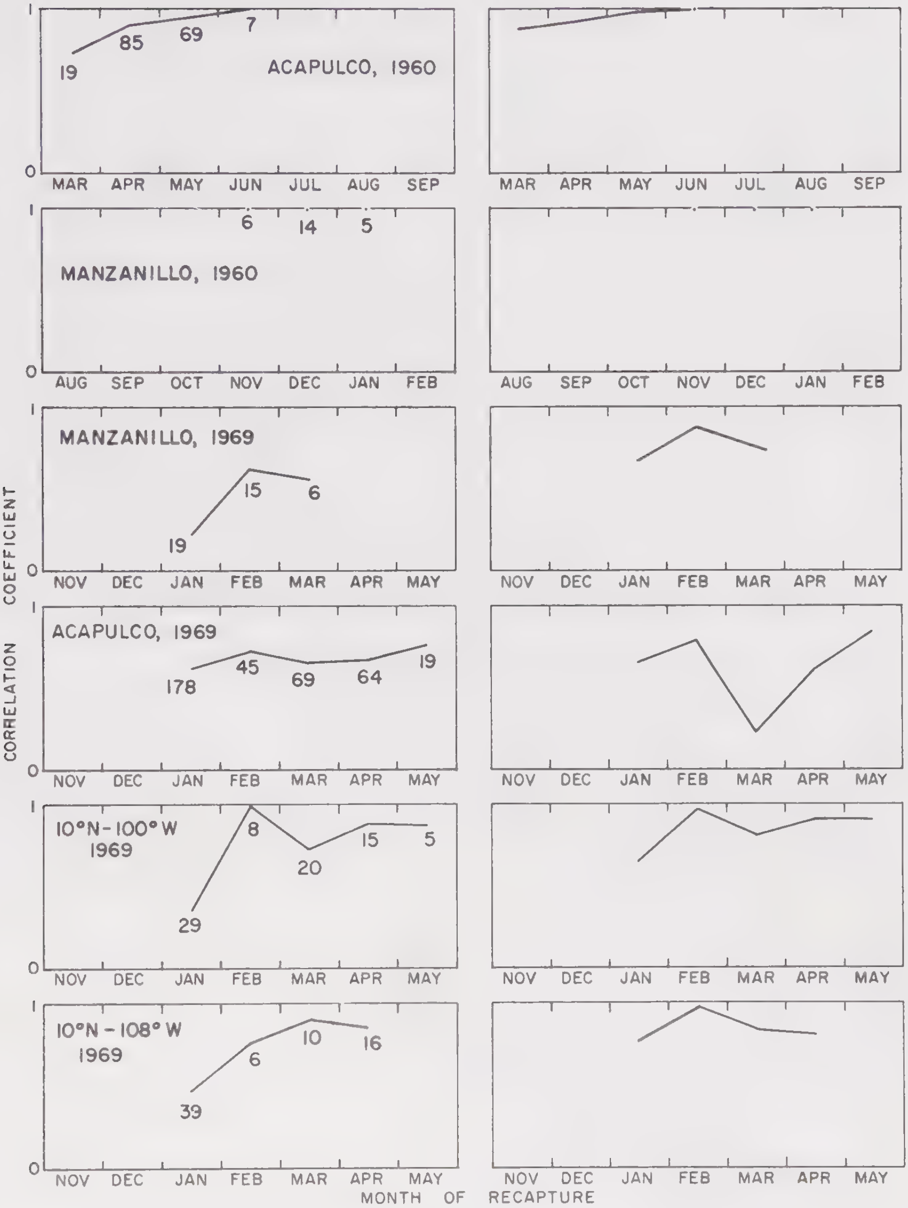


FIGURE 10. Unadjusted (left side of figure) and adjusted (right side of figure) correlation coefficients, by months of recapture.

FIGURA 10. Coeficientes de correlación sin ajustar (margen izquierdo de la figura) y ajustados (margen derecho de la figura), por meses de recaptura.

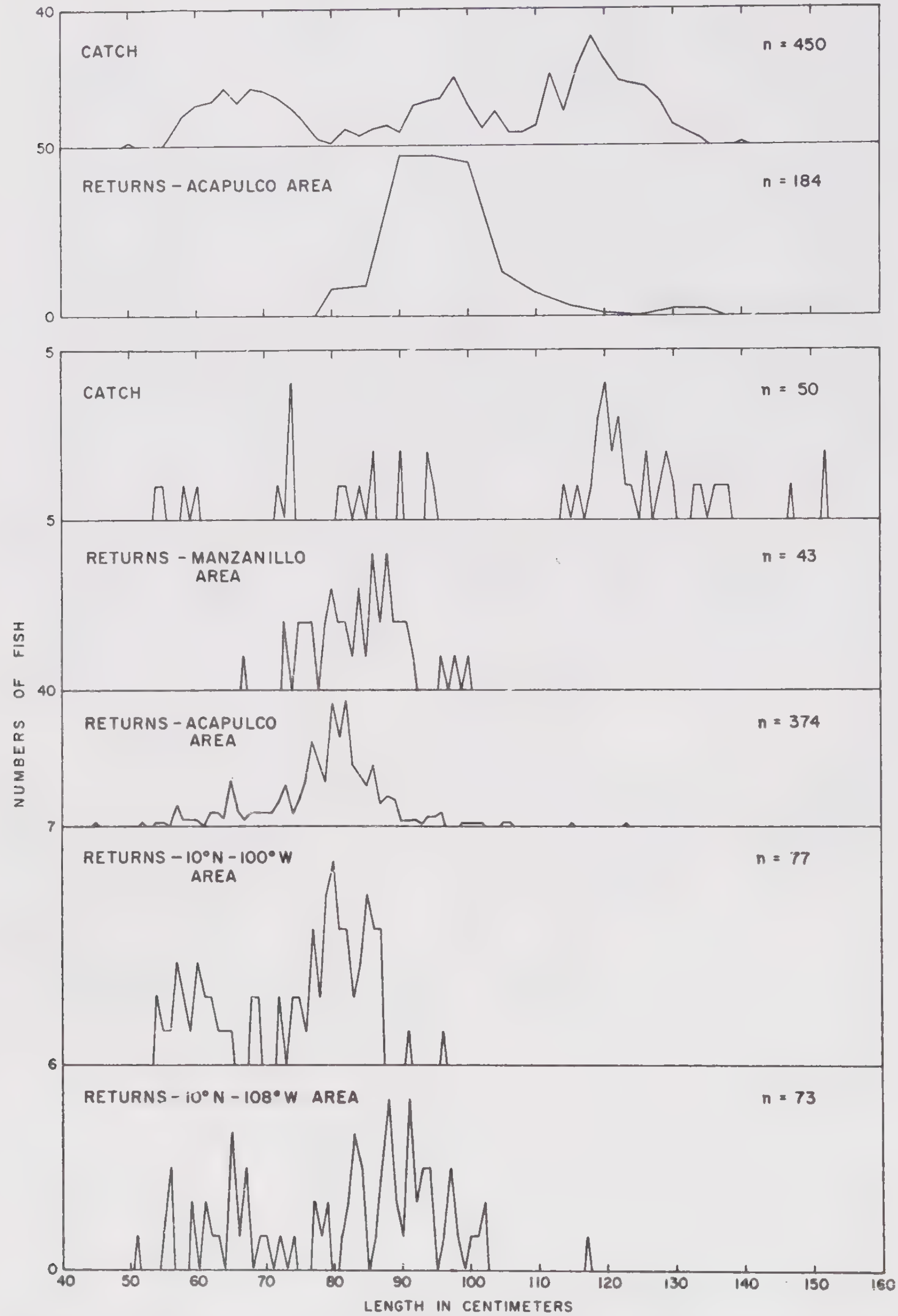


FIGURE 11. Distributions of the lengths of samples of fish in the catches and of the lengths at the times of release of the tagged fish which were returned.

FIGURA 11. Distribución de tallas de las muestras de peces en las capturas y de las tallas a tiempo de liberación de los peces marcados que fueron devueltos.

TABLE 1. Tagged fish release and return data used for studies of the migrations of yellowfin off the southern coast of Mexico.

TABLA 1. Datos de liberación y de devolución de peces marcados usados para estudiar las migraciones de aleta amarilla frente a la costa meridional de México.

Cruise	**Dates of release**	**Vessel**	**Vessel type**	**Region**	**Number released**	**Number returned**
Crucero	**Fechas de liberación**	**Barco**	**Tipo de barco**	**Región**	**Cantidad liberada**	**Cantidad devuelta**
1033	Mar. 26-Apr. 9, 1960	*Julia B.*	chartered baitboat cliper fletado	Acapulco	1,141	190
1035	Aug. 24-27, 1960	*Westport*	baitboat	Manzanillo	345	32
1055	Oct. 25-27, 1969	*Connie Jean*	chartered	Manzanillo	436	49
	Oct. 28-Nov. 4, 1969		purse seiner cerquero	Acapulco	4,734[1]	430
	Nov. 12-14, 1969		fletado	10°N-100°W	1,714[2]	107
	Nov. 7-9 and 16-19, 1969			10°N-100°W	1,636	89

[1] includes six re-releases — incluye seis reliberaciones

[2] includes five re-releases — incluye cinco reliberaciones

TABLE 2. Effort data for the 5-degree areas in which fish of the 1960 releases were recaptured. The notation is as follows: f_{PSPS}, purse-seine effort in Class-3 purse-seine days; f_{BBBB}, baitboat effort in Class-4 baitboat days; f_{BBPS}, baitboat effort converted to Clase-3 purse-seine days; $f_{(PS+BB)PS}$, total effort in Class-3 purse-seine days.

TABLA 2. Datos del esfuerzo por áreas de 5 grados en las que los peces liberados en 1960 fueron recapturados. La anotación es la siguiente: f_{PSPS}, esfuerzo por cerqueros en días de la clase 3 de cerqueros; f_{BBBB}, esfuerzo de clipers en días de la clase 4 de clipers; f_{BBPS}, esfuerzo de clipers convertido en días de la clase 3 de cerqueros; $f_{(PS+BB)PS}$, esfuerzo total en días de la clase 3 de cerqueros.

5-degree area Area de 5 grados		1960										1961				
		Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
0-10-090	f_{PSPS}		74.8	78.0	110.5	61.7	235.6	79.6	89.7	408.5	49.1	4.0	819.1	445.4	550.9	340.3
	f_{BBBB}	99.5	6.3	18.4	37.4	26.9	23.1	11.0	2.5	8.4	7.6	46.1	39.8	8.6	0.8	
	f_{BBPS}	55.7	3.0	10.1	20.6	14.3	11.8	6.3	1.4	3.8	3.5	22.1	20.7	3.6	0.4	
	$f_{(PS+BB)PS}$	55.7	77.8	88.1	131.1	76.0	247.4	85.9	91.1	412.3	52.6	26.1	839.8	449.0	551.3	340.3
0-10-095	f_{PSPS}	22.6	7.4	1.4	6.2				3.7	23.2	160.4	377.8	24.5	3.3	10.4	41.0
	f_{BBBB}	12.2	19.8	28.7	11.3	1.3				2.5	2.3	13.0	4.6	2.4	1.6	
	f_{BBPS}	6.8	9.3	15.8	6.2	0.7				1.1	1.1	6.2	2.4	1.0	0.9	
	$f_{(PS+BB)PS}$	29.4	16.7	17.2	12.4	0.7			3.7	24.3	161.5	384.0	26.9	4.3	11.3	41.0
0-15-095	f_{PSPS}	36.1	90.2	39.1	128.3	14.5	19.8	13.7	46.8	336.8	475.3	681.9	241.5	79.5	76.9	61.1
	f_{BBBB}	18.5	40.5	65.4	15.4	3.8	4.4	2.5		12.6	10.2	13.0	9.5	2.4	0.8	
	f_{BBPS}	8.7	20.3	25.3	8.5	1.7	2.1	1.2		6.2	4.7	6.0	4.3	1.2	0.4	
	$f_{(PS+BB)PS}$	44.8	110.5	74.4	136.8	16.2	21.9	14.9	46.8	343.0	480.0	687.9	245.8	80.7	77.3	61.1
0-15-100	f_{PSPS}	204.3	91.5	330.2	160.2	18.6	21.9	10.9	60.5	63.3	150.6	158.2	155.2	77.8	143.9	172.4
	f_{BBBB}	26.4	20.9	52.5	11.8	3.8	6.9	3.8		20.8	21.1	2.4	22.5	1.7		
	f_{BBPS}	12.4	10.4	28.4	6.5	1.7	3.3	1.7		10.2	9.7	1.1	10.1	0.8		
	$f_{(PS+BB)PS}$	216.7	101.9	358.6	166.7	20.3	25.2	12.6	60.5	73.5	160.3	159.3	165.3	78.6	143.9	172.4
0-20-105	f_{PSPS}	459.1	515.7	261.3	144.7	23.3	21.4	6.8	18.9	11.7	6.9	39.0	35.6	369.7	556.6	160.4
	f_{BBBB}	1.3	8.0	12.4	7.1	2.5	4.4	3.3	7.9	2.8	20.7	64.9	59.9	52.9	7.2	5.6
	f_{BBPS}	0.6	4.0	6.7	3.9	1.1	2.1	1.5	3.5	1.4	9.5	29.9	27.0	26.5	3.2	2.2
	$f_{(PS+BB)PS}$	459.7	519.7	268.0	148.6	24.4	23.5	8.3	22.4	13.1	16.4	68.9	62.6	396.2	559.8	162.6

TABLE 3. Effort data for the 5-degree areas in which fish of the 1969 releases were recaptured. The notation is defined in Table 2.

TABLA 3. Datos del esfuerzo por áreas de 5 grados en las que los peces liberados en 1969 fueron recapturados. La anotación se explica en la Tabla 2.

5-degree area		1970											
Area de 5 grados		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
0-00-080	f_{PSPS}	34.1	31.5	10.8	156.6	33.2	23.2	5.8					
0-00-110	f_{PSPS}				22.4	112.9	0.8				8.3	79.7	11.6
0-05-085	f_{PSPS}	82.4	173.9	224.8	181.4	120.9	14.9	9.1					
	f_{BBBB}	3.5	10.6	2.4									
	f_{BBPS}	1.2	5.5	1.6									
	$f_{(PS+BB)PS}$	83.6	179.4	226.4	181.4	120.9	14.9	9.1					
0-05-090	f_{PSPS}	109.2	23.5	187.3	283.4	220.5		0.8					
0-05-095	f_{PSPS}	179.7	18.8	162.0	257.5	6.6		5.0					
0-05-100	f_{PSPS}	105.6	16.6	21.5	217.1		1.2					16.6	
0-05-105	f_{PSPS}	91.4	15.3	8.3	27.3		0.8					10.0	
0-05-130	f_{PSPS}						81.3	48.1	81.0	93.6	93.2	126.8	16.6
0-05-140	f_{PSPS}						11.6	4.2	5.0	3.3			
0-10-090	f_{PSPS}	68.9	21.1	14.0	19.9	11.1	1.1						
0-10-095	f_{PSPS}	379.4	36.2	156.7	152.3		1.2						
0-10-100	f_{PSPS}	323.0	69.7	157.9	476.5	1.7						10.0	
0-10-105	f_{PSPS}	322.2	95.3	61.1	156.8	4.0					0.8	10.0	
	f_{BBBB}	17.0		2.0									
	f_{BBPS}	5.8		1.3									
	$f_{(PS+BB)PS}$	328.0	95.3	62.4	156.8	4.0					0.8	10.0	
0-10-120	f_{PSPS}					19.1	24.1	5.0	45.7	244.9	433.7	276.1	
0-10-125	f_{PSPS}					1.7	6.6	1.7	298.8	231.4	121.9	69.6	
0-10-130	f_{PSPS}						1.7	31.5	123.6	74.9	47.2	8.3	
0-15-095	f_{PSPS}	57.7	21.3	8.6	50.4	8.5	2.2						
0-15-100	f_{PSPS}	294.7	223.4	185.9	124.2	12.9	2.1					1.7	

TABLE 3. (Continued)
TABLA 3. (Continuación)

5-degree area Area de 5 grados		1970											
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
0-15-105	f_{PSPS}	210.6	537.8	246.3	180.7	61.1	1.2					5.0	1.7
	f_{BBBB}		1.0	1.0									
	f_{BBPS}		0.6	0.4									
	$f_{(PS+BB)PS}$	210.6	538.4	246.7	180.7	61.1	1.2					5.0	1.7
0-15-110	f_{PSPS}	136.3	41.8	132.4	148.9	52.5					5.0		
	f_{BBBB}	87.1	64.5	56.0	31.7	15.8							
	f_{BBPS}	40.9	36.8	25.2	9.8	7.1							
	$f_{(PS+BB)PS}$	177.2	78.6	157.6	158.7	59.6					5.0		
0-20-105	f_{PSPS}	248.2	823.9	595.0	361.4	33.8	14.5						3.3
	f_{BBBB}	10.4	34.6	16.5	58.7	1.5							
	f_{BBPS}	48.9	19.7	7.4	18.2	0.7							
	$f_{(PS+BB)PS}$	297.1	843.6	602.4	379.6	34.5	14.5						3.3
0-20-110	f_{PSPS}	34.3	31.0	79.4	37.5	179.1							1.7
	f_{BBBB}	55.6	21.0	73.4	85.5	20.4							
	f_{BBPS}	26.1	12.0	33.0	26.5	9.2							
	$f_{(PS+BB)PS}$	60.4	43.0	112.4	64.0	188.3							1.7
0-25-110	f_{PSPS}	5.4	13.7	8.7	5.7	5.8							
	f_{BBBB}	30.6	69.1	19.3	0.6								
	f_{BBPS}	14.4	39.4	8.7	0.2								
	$f_{(PS+BB)PS}$	19.8	53.1	17.4	5.9	5.8							
0-25-115	f_{PSPS}	4.0	3.0	1.7									
	f_{BBBB}	1.6											
	f_{BBPS}	0.8											
	$f_{(PS+BB)PS}$	4.8	3.0	1.7									

TABLE 4. Tag return (n_{ij}), total logged effort (f_{ij}), and adjusted tag return (N_{ij}) data for 1970 for eight areas of the eastern Pacific Ocean. The areas are shown in Figure 3.

TABLA 4. Devolución de marcas (n_{ij}), esfuerzo total registrado (f_{ij}) y datos ajustados de la devolución de marcas (N_{ij}) en 1970 correspondiente a ocho áreas del Océano Pacífico oriental. Las áreas se presentan en la Figura 3.

	Area 1			Area 2			Area 3			Area A			Area B			Area C			Area D			Outside CYRA			Total
	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}	f_{ij}	N_{ij}	n_{ij}
Jan.	0	85.0	0.0	9	297.1	19.6	1	212.9	3.0	247	1,970.1	81.1	8	308.9	16.8	0	64.7	0.0	0	71.8	0.0	0	0.0	—	
Feb.	0	99.4	0.0	37	843.6	28.4	2	85.5	15.1	28	1,035.0	17.5	8	259.4	19.9	0	0.8	0.0	0	62.5	0.0	0	0.0	—	
Mar.	0	130.3	0.0	9	604.7	9.6	1	166.1	3.9	78	1,010.0	50.0	16	491.5	21.1	0	14.5	0.0	0	19.9	0.0	0	0.0	—	
Apr.	0	64.2	0.0	2	420.6	3.1	2	159.9	8.1	66	1,642.8	26.0	27	571.5	30.5	0	20.1	0.0	2	199.0	6.5	0	23.2	0.0	
May	3	194.1	10.0	0	34.5	0.0	6	59.6	65.2	3	94.8	20.4	14	392.7	23.1	0	0.6	0.0	0	49.5	0.0	2	242.5	5.3	
Jun.	0	0.0	—	1	14.5	44.6	0	0.0	—	0	8.7	0.0	2	28.8	44.9	0	5.9	0.0	0	55.5	0.0	0	308.0	0.0	
Jul.	0	0.0	—	0	0.0	—	0	0.0	—	0	5.0	—	0	11.6	—	0	1.7	—	0	11.6	—	1	257.4	—	
Aug.	0	0.8	—	0	0.0	—	0	0.0	—	0	0.0	—	0	0.0	—	0	0.0	—	0	0.0	—	2	701.2	—	
Sep.	0	0.0	—	0	0.0	—	0	0.0	—	0	0.0	—	0	0.0	—	0	5.0	—	0	0.0	—	1	881.4	—	
Oct.	0	0.0	—	0	0.0	—	1	5.0	—	0	0.8	—	0	0.0	—	0	27.4	—	0	0.0	—	1	902.1	—	
Nov.	0	0.0	—	0	0.0	—	0	0.0	—	0	53.3	—	0	0.0	—	0	8.4	—	0	0.0	—	0	777.2	—	
Dec.	0	1.7	0.0	0	3.3	0.0	0	0.0	—	0	1.7	—	0	0.0	—	0	0.0	—	0	0.0	—	0	41.5	—	
Total	3	575.5	18.3	58	2,218.3	91.9	13	689.0	66.3	422	5,822.2	254.8	75	2,065.4	127.7	0	149.1	0.0	2	469.8	15.0	7	4,134.5	6.0	580

MIGRACIONES DEL ATUN ALETA AMÀRILLA MARCADO FRENTE A LA COSTA MERIDIONAL DE MEXICO EN 1960 Y 1969

por

William H. Bayliff y Brian J. Rothschild[1]

EXTRACTO

El método de mapas, el de Jones, el de la variancia-covariancia y el de Skellam fueron empleados para estudiar las migraciones del atún aleta amarilla marcado y liberado frente a la costa meridional de México en 1960 y 1969. Los tres primeros métodos son todos útiles, y cada uno presenta información que complementa la presentada por los otros. El método de Skellam, conforme se usa en este informe, es menos útil.

Parece que los desplazamientos de los peces marcados y liberados en 1960 hubieran sido fuertemente orientados, pero ésto probablemente fue causado principalmente por la distribución del esfuerzo de pesca. El esfuerzo se distribuyó más extensamente en 1970, y parece que los desplazamientos de los peces liberados en 1969 fueran menos orientados. Los coeficientes de correlación derivados del método variancia-covariancia indicaron, sin embargo, que no eran aleatorios.

Los peces pequeños liberados en las áreas de Acapulco y los 10°N-100°W en 1969 migraron al área de Manzanillo a principios de febrero 1970. Los peces medianos y grandes liberados en las mismas áreas en el mismo año tuvieron, sin embargo, la tendencia a desplazarse al sudeste durante el primer semestre de 1970.

INTRODUCCION

Las migraciones de atún aleta amarilla, *Thunnus albacares*, en el Océano Pacífico oriental han sido estudiadas por Blunt y Messersmith (1960), Schaefer, Chatwin y Broadhead (1961) y Fink y Bayliff (1970); el último informe incluye los datos de todos los peces marcados y liberados antes de 1965. Casi todo el marcado de aleta amarilla frente a la costa meridional de México hasta esa época se realizó en dos cruceros conducidos en 1960. A mediados y a fines del decenio de 1960 la pesca se extendió mar adentro, especialmente entre el ecuador y los 15°N (Calkins y Chatwin, 1967 y 1971), y durante los períodos de veda de la pesca de aleta amarilla en el área reglamentaria de la Comisión de aleta amarilla (ARCAA) (Figura 1) la pesca se había realizado al oeste de esta área. Por esta razón se llevó a cabo otro marcado en 1969 frente a la costa meridional de México, tanto cerca de la costa como mar adentro. Este informe es un análisis de los experimentos de 1960 y 1969, en el que se emplean nuevos métodos además de los usados en informes previos.

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Los programas computadores usados en este informe fueron escritos o modificados por el Dr. Robert C. Francis, la Srta. JoAnne Levatin y los Sres. Christopher T. Psaropulos y Donald L. Whitt. El manuscrito fue examinado por los Dres. James Joseph, Robert C. Francis y Jerome J. Pella.

MATERIALES Y METODOS

Los métodos de marcado de los peces y el empleo de los datos de la devolución de marcas son descritos por Fink (1965), Fink y Bayliff (1970) y Bayliff (1973). (Las palabras "devolver" y "devolución" (Jones, 1966: xiii) en este informe substituyen "retornar" y "retorno" definidas por Fink y Bayliff (1970: 155). Los métodos de colectar y utilizar las estadísticas de captura y esfuerzo son discutidos por Shimada y Schaefer (1956), Joseph y Calkins (1969) y Bayliff (1971).

La mayoría de los cálculos se realizó en las computadoras CDC 3600 y Burroughs 6700 en la Universidad de California en San Diego. Se emplearon para este propósito los Programas CIAT F04 (Psaropulos, 1966) y otros dos inéditos.

DATOS USADOS

Liberaciones y devoluciones de marcas

Se usan en este informe los datos solamente de tres cruceros, ya que no se han obtenido más de nueve devoluciones de marcas de cualquier otro crucero conducido en esta área. Los datos de liberación y devolución de estos cruceros se enumeran en la Tabla 1. No se emplearon todos los datos de devoluciones, ya que algunos fueron inapropiados debido a que no se conocía el área o la fecha de recaptura o por cualquiera otra razón. Se ha llevado a cabo algún marcado cerca a las Islas Revillagigedo y cerca a la Isla Clipperton, pero estos peces se comportaron diferentemente a los marcados más lejos de las islas, ya que muchos de ellos permanecen aparentemente cerca de las islas por períodos considerables de tiempo (Fink y Bayliff, 1970). Como la mayoría de la captura frente a la costa meridional de México se obtiene en áreas que no están en la vecindad de estas islas, no se consideran en este informe los datos de los experimentos del marcado conducidos cerca a estas islas. Las áreas en las que se liberaron los peces marcados se presentan en la Figura 2.

Estadísticas de pesca

Los datos estadísticos obtenidos rutinariamente por la Comisión del Atún incluyen las capturas registradas en toneladas americanas (cortas) de atún aleta amarilla por áreas de 1 grado y 5 grados, por meses, trimestres y años, por tipo de arte (cerqueros y clípers) y por la clase de capacidad de los barcos, y el esfuerzo correspondiente en días de pesca, no normalizado y normalizado a días de la Clase 3 de barcos cerqueros (barcos de 101-200 toneladas americanas de capacidad) y a días de la Clase 4 de clípers (barcos de carnada de 201-300 toneladas americanas de capacidad) (Shimada y Schaefer, 1956; Joseph y Calkins, 1969). Los datos del esfuerzo obtenidos por la Comisión del Atún representan aproximadamente el 90 por ciento del esfuerzo total correspondiente a los períodos de referencia y se supone que tengan la misma distribución por área y tiempo que el esfuerzo total. En cada año desde 1966 ha existido una cuota de captura de aleta amarilla en el ARCAA, y la mayoría de los barcos que zarpan cada año después de la fecha de clausura tienen un límite respecto a la porción de aleta amarilla de los peces desembarcados por las capturas obtenidas en el ARCAA. El esfuerzo ejercido en el ARCAA por barcos que zarparon después de la fecha de veda se denomina "esfuerzo reglamentado", y estos datos se mantienen aparte de los datos del "esfuerzo no reglamentado". Se supone que todo el esfuerzo no reglamentado se dirige hacia el aleta amarilla (y también hacia el barrilete) excepto en unos pocos viajes en que otras especies que no fueron aleta amarilla o barrilete formaron más de un tercio del peso total de la captura. No se emplean en este estudio los datos del esfuerzo reglamentado.

Es necesario obtener estimaciones del esfuerzo de pesca en cada estrato de área de 5 grados y mes en que se han recapturado peces marcados. Los datos del esfuerzo se convirtieron todos a unidades de la Clase 3 de cerqueros por el método de Bayliff (1971), usando datos separados para la captura por unidad de esfuerzo de los clípers correspondiente a los 0°-15°N y norte de los 15°N. El esfuerzo mensual de cerqueros y clípers, y de ambas artes combinadas, en las áreas donde se recapturaron peces marcados se presentan en la Tabla 2 para marzo 1960-mayo 1961 y en la Tabla 3 para enero-diciembre 1970. Las áreas de 5 grados se codifican por las latitudes y longitudes de sus márgenes sudestes, precedidas por 0's para áreas al norte del ecuador o 2's para áreas al sur del ecuador (Shimada y Schaefer, 1956). No hubo esfuerzo sin reglementar en el

ARCAA durante octubre-diciembre 1969, y todas menos una de las marcas devueltas durante este período fueron de peces recapturados por el barco de marcado.

RESULTADOS

Los estratos área-tiempo en los que los peces marcados son recapturados dependen no solamente en las migraciones de los peces, sino también en la distribución del esfuerzo de pesca. Si un pez marcado es liberado en un área la probabilidad de que sea recapturado en otra depende no solamente en el esfuerzo de pesca en la segunda área, pero también en el de la primera área y en todas las áreas por las que el pez pasó mientras viaja de la primera a la segunda área. La mayoría de los análisis en este informe de las migraciones de peces marcados se realiza de dos formas, sin ajustes y con ellos para encontrar las diferencias en las cantidades del esfuerzo de pesca en los diferentes estratos de área de 5 grados y mes donde se efectúa la recaptura. Estos ajustes se hicieron al dividir el número de devoluciones en cada estrato de área de 5 grados y mes por el correspondiente esfuerzo y luego multiplicándolo por un factor para obtener una cantidad ajustada de recapturas. Los cálculos se explican detalladamente en los últimos capítulos de este informe.

El método de ajuste es inadecuado, ya que no se hace concesión alguna por las cantidades de esfuerzo de pesca en los estratos área-tiempo por el que pasan los peces antes de su recaptura. Tales ajustes pueden probablemente llevarse a cabo solo mediante la simulación computadora. Sin embargo, es probablemente mejor tener mientras tanto el ajuste que se acaba de describir a no tener ninguno.

Métodos incluyendo mapas

Las localidades de recaptura de los peces de cada grupo liberado se presentan en la Figura 2. Estos mapas ofrecen un indicio útil sobre las distancias y las direcciones recorridas, pero no definen estos parámetros en términos cuantitativos. Además, no existe ninguna medida para indicar las fechas de recaptura o los tiempos en libertad, y ésto se puede obtener solo al substituir varios mapas por cada uno de los actuales.

En la Figura 3 y la Tabla 4 se indican los números ajustados de devoluciones en ocho áreas arbitrariamente seleccionadas de peces liberados en 1969 en un área de 15 grados (Area A en la figura). Los números se calcularon por

$$N_{ij} = \left(\frac{n_{ij}}{f_{ij}}\right)\left(\frac{\sum_i \sum_j n_{ij}}{\sum_i \sum_j \frac{n_{ij}}{f_{ij}}}\right) \qquad (1)$$

donde

N_{ij} = cantidad ajustada de devoluciones en área i durante el mes j,
n_{ij} = cantidad actual de devoluciones en área i durante el mes j y
f_{ij} = esfuerzo en área i durante el mes j.

Las cuatro devoluciones de peces liberados al norte de los 20°N no se usaron para estos cálculos, pero se emplearon seis de las cuáles se conocían las áreas de 5 grados de recaptura pero no las de 1 grado. Es evidente que relativamente pocos peces marcados y liberados en el área de referencia de 15 grados migraron a áreas al oeste de Baja California, fuera del ARCAA o al de los 5°N. Parece según estos datos que los peces marcados y liberados en el Area A se desplazaron del Area A al Area 2 a principios de febrero y regresaron al Area A aproximadamente a fines del mes. La incidencia de los peces marcados y liberados en el Area A aumentó en el Area B de enero a mayo, indicando el desplazamiento de los peces liberados en el Area A al Area B durante este período.

Método de Skellam

Los promedios de las distancias cuadradas del desplazamiento se calculan mediante

$$\overline{r_j^2} = \left(\sum^{n_j} r_j^2\right) \Big/ n_j \qquad (2)$$

donde

$\overline{r_j^2}$ = promedio de las distancias cuadradas del desplazamiento de los peces recapturados en el mes j,
r_j = distancia del desplazamiento de un pez recapturado en el mes j y
n_j = cantidad de devoluciones de peces en el mes j.

Los promedios ajustados de las distancias cuadradas del desplazamiento se calculan mediante

$$\overline{R_j^2} = \sum^{n_j} \left(\frac{r_{ij}^2}{f_{ij}}\right) \Big/ \sum^{n_j} \left(\frac{1}{f_{ij}}\right) \qquad (3)$$

donde

$\overline{R_j^2}$ = promedio ajustado de las distancias cuadradas del desplazamiento de los peces recapturados en el mes j,
r_{ij} = distancia del desplazamiento de un pez recapturado en el área i durante el mes j y
f_{ij} = esfuerzo en el área i durante el mes j.

Skellam (1951) indicó que si la dispersión es aleatoria los promedios de las distancias cuadradas del desplazamiento aumentan linealmente con el tiempo. Sin embargo, si el punto de liberación es cerca a la costa los peces irán solo por una corta distancia en esa dirección, y parece que el índice de dispersión disminuye con el tiempo aún si éste no es el caso.

Los promedios sin ajustar de las distancias cuadradas de desplazamiento de los seis grupos ya referidos de liberaciones se presentan en el margen izquierdo de la Figura 4. Los puntos se grafican solo para los meses que incluyen por lo menos cinco recapturas. Las cifras cerca a los puntos indican la cantidad de recapturas en cada mes. Estos datos indican que la dispersión es aproximadamente aleatoria. En el área de Manzanillo la cantidad de devoluciones fue relativamente alta y el valor de $\overline{r_j^2}$ fue relativamente bajo en febrero 1970, siendo lo contrario para las áreas de Acapulco y los 10°N-100°W. Esto se debe probablemente a que el esfuerzo durante ese mes fue relativamente alto en las áreas 0-15-105 y 0-20-105 y relativamente bajo en las áreas 0-10-095, 0-10-100 y 0-10-105 (Tabla 4).

Los promedios ajustados de las distancias cuadradas del desplazamiento se presentan en el margen derecho de la Figura 4. Estos gráficos son muy similares a los del margen izquierdo de la figura. Los valores $\overline{R_j^2}$ de febrero 1970 de las áreas de Acapulco y 10°N-100°W son relativamente altos, lo cuál indica que en promedio los peces se encontraban más lejos de las áreas de liberación durante febrero que durante enero o marzo. Los datos indican la presencia de peces de esas dos áreas en el área de Manzanillo durante febrero, así que es lógico suponer que el alto esfuerzo ejercido en esa área durante ese mes se debió por lo menos parcialmente a una afluencia de peces de las áreas de Acapulco y los 10°N-100°W.

Si el desplazamiento ocurre en su mayor parte o todo en una dirección y en base continua los promedios de los distancias del desplazamiento aumentarían linealmente con el tiempo, y los promedios de las distancias cuadradas del desplazamiento aumentarían exponencialmente. En la próxima sección se indicará que los peces de las liberaciones de 1960 fueron recapturados en su mayoría al desplazarse en una dirección, y puede verse que los gráficos de los peces liberados en el área de Acapulco en 1960 son cóncavos hacia arriba y por lo tanto aproximadamente exponenciales.

Método de Jones

Este método, concebido por Jones (1959 y 1966), ha sido usado anteriormente en una forma ligeramente diferente para el aleta amarilla por Fink y Bayliff (1970).

La dispersión de los peces se analiza según los datos de los meses de recaptura, días en libertad, distancias de desplazamiento y direcciones de desplazamiento. Se emplean ocho direcciones de desplazamiento, 0°-45° real = 0, 45°-90° real = 1, . . . y 315°-360° real = 7.

Se hacen los siguientes cálculos respecto a los datos no ajustados por donde

V_{jk} = promedio ajustado de la velocidad de dislocación de peces recapturados en el mes j que se desplazaron en dirección k y

$$A_{jk}^2 = \frac{1}{\sum_{i}^{n_{jk}} (1/f_{ij})} \left[\sum_{i}^{n_{jk}} \frac{r_{ijk}^2}{t_{ijk}\, f_{ij}} - \frac{\left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \sin \Theta_k \right)^2 + \left(\sum_{i}^{n_{jk}} \frac{r_{ijk}}{f_{ij}} \cos \Theta_k \right)^2}{\sum_{i}^{n_{jk}} \left(\frac{t_{ijk}}{f_{ij}} \right)} \right] \qquad (12)$$

donde

A_{jk}^2 = media cuadrada ajustada del coeficiente de dispersión de los peces recapturados en el mes j que se desplazaron en dirección k.

El significado del promedio de la velocidad de dislocación y de la media cuadrada del coeficiente de dispersión ha sido discutido por Jones (1959 y 1966). En resumen, la primera pertenece al desplazamiento direccional y la última al desplazamiento aleatorio. La última es una medida del promedio de la cantidad de desviación del promedio de dirección del desplazamiento. Un valor alto de $v_{j\cdot}$ (o $V_{j\cdot}$) y un valor bajo de $a_{j\cdot}$ (o $A_{j\cdot}$) indicarían desplazamiento direccional con poca dispersión, mientras un valor bajo de $v_{j\cdot}$ (o $V_{j\cdot}$) y un valor alto de $a_{j\cdot}$ (o $A_{j\cdot}$) indicarían lo contrario. Aún si el desplazamiento es completamente aleatorio, no se esperaría que los valores de $v_{j\cdot}$ (o $V_{j\cdot}$) fueran iguales a 0 en la mayoría de los grupos actuales de liberaciones porque se hicieron cerca al litoral, y los peces se encontraban limitados en sus movimientos hacia la costa.

Las direcciones y los promedios de las distancias de desplazamiento, según fueron calculadas por los datos no ajustados de devolución, se presentan en el margen izquierdo de los diagramas de la Figura 5. La cifra en el centro del primer diagrama indica la cantidad de peces que no se desplazaron de las localidades de liberación. (Como lo explicaron Schaefer, Chatwin y Broadhead (1961), debido a la falta de precisión en anotar las posiciones en el mar, los peces que se desplazaron 10 o 20 millas se registran frecuentemente como si hubieran sido recapturados en la localidad de liberación). Las cifras cerca a las puntas de las flechas indican la cantidad de peces que se desplazaron en cada dirección y el promedio de las distancias de desplazamiento, respectivamente. La anchura del círculo y de las líneas son proporcionales a los porcentajes de los peces que fueron recapturados en las localidades de liberación y a los porcentajes que se desplazaron en cada dirección. La longitud de las líneas es proporcional al promedio de las distancias de desplazamiento.

Los peces liberados en el área de Acapulco en 1960 se recapturaron principalmente al noroeste, mientras que los liberados en el área de Manzanillo en 1960 y en las áreas de Manzanillo y Acapulco en 1969 parece que hubieran migrado en su mayoría hacia el sudeste. Los peces liberados mar adentro fueron recapturados principalmente al este y nordeste. Los promedios de las distancias de desplazamiento de los peces liberados en el área de Acapulco en 1960 fueron inferiores a los de los peces de otros grupos de liberaciones. En la Figura 4 puede verse que la mayoría de los primeros fueron recapturados poco tiempo después de haber sido liberados, mientras que la mayoría de los últimos estuvieron más tiempo en libertad, así que el promedio de la velocidad de dislocación no es necesariamente inferior respecto a los peces liberados en 1960 en el área de Acapulco.

Los diagramas equivalentes a los que se encuentran en el margen izquierdo de la Figura 5 se presentan para los datos ajustados de devolución en el margen derecho de la figura. Los resultados son bastante similares a los obtenidos respecto a los datos no ajustados. Parece que hubo una migración considerable en Dirección 6 en el área de los 10°N-108°W, pero en el margen izquierdo de la figura puede verse que ésto se basa en solo tres recapturas, junto con un esfuerzo relativamente pequeño de pesca en los estratos correspondientes de área de 5 grados y mes.

Parece que las migraciones estuvieron más orientadas para los peces liberados en 1960 que para aquellos liberados en 1969. Con el fin de investigar ésto aún más se graficaron las distribuciones del esfuerzo de pesca y las devoluciones por áreas de 1 grado y meses. Estos datos indicaron más claramente que los de la Tabla 2 que hubo relativamente poco esfuerzo al sudeste del área de Acapulco, y especialmente al noroeste del área de Manzanillo, durante los meses en los que se recapturó la mayor parte de los peces marcados. Por lo consiguiente existen dos posibilidades, (1) que el desplazamiento estuvo fuertemente orientado, lo que causó que el esfuerzo fuera distribuido en la forma en que lo fue, o (2) que la distribución del esfuerzo fue la causa de que el desplazamiento pareciera fuertemente orientado, aunque éste no fue el caso. La primera explicación es la más probable si la distribución de los peces marcados durante los períodos después de la liberación fue aproximadamente igual a la de la mayoría de los peces en la misma área general y si el tiempo permitió que los barcos pescaran donde había más concentración de peces. La última explicación es más probable si la distribución del esfuerzo de pesca fue el resultado de distribuciones de peces distintos a aquellos de los grupos a los que pertenecían los peces marcados o el resultado de condiciones meteorológicas pos las cuáles los barcos evitaron algunas de las áreas en las que se desplazaron los peces marcados. En general, el tiempo es bastante malo entre Acapulco y Manzanillo de julio a fines de octubre, entre Costa Rica y Manzanillo de agosto a fines de octubre y en el Golfo de Tehuantepec de noviembre a fines de marzo. El esfuerzo de pesca siempre ha sido relativamente bajo en el Golfo de Tehuantepec. Los resultados de los experimentos de 1969 indicaron que el desplazamiento fue probablemente más aleatorio de lo que indicaron los datos respecto a los peces de los experimentos de 1960. Esto modifica la conclusión de Fink y Bayliff (1970), quienes basados en los resultados obtenidos con datos sin ajustar por el método de Jones declararon que el desplazamiento de los peces liberados en 1960 estuvo fuertemente orientado.

No existe ninguna clave en estos diagramas que indiquen el tiempo en que estuvieron en libertad los peces o las fechas de recaptura, y ésto puede obtenerse solo substituyendo varios diagramas por cada uno de los actuales.

Las direcciones y los promedios de las distancias de desplazamiento por mes de recaptura, según se calculan por los datos de devolución no ajustados, se presentan en el margen izquierdo de la Figura 6. Los datos de los peces que se desplazan en diferentes direcciones se muestran en distintos recuadros en cada gráfico. Los puntos de meses consecutivos se juntan por medio de líneas sólidas y aquellos de meses no consecutivos por líneas de trazos. Las cifras cerca a los puntos indican la cantidad de peces en cada mes. Los valores de $v_{\cdot k}$ aparecen en todos los recuadros, y los valores de $a_{\cdot\cdot}^2$ al pie de los recuadros. Estos diagramas son útiles para descubrir migraciones estacionales. Por ejemplo, si los peces estuvieran en el extremo meridional de su distribución en enero y en el extremo septentrional en julio, y hubieran sido marcados en enero, $\overline{r}_{j\cdot}$ aumentaría por unos 6 meses y luego se reduciría. Además, habría muchos peces en los recuadros en las Direcciones 0 y 7 y pocos en los recuadros de las Direcciones 3 y 4 durante febrero-junio, mientras que lo contrario sería verdad durante agosto-diciembre. Las migraciones estacionales no son aparentes; las distancias desde las localidades de liberación solo tienen la tendencia a ser constantes o aumentar con el tiempo. Las velocidades en cada dirección fueron aproximadamente las mismas en todos los experimentos, pero las velocidades al pie de los recuadros en los experimentos de 1960 fueron superiores debido a que la mayoría de los peces que fueron recapturados se habían desplazado en las mismas direcciones.

Los diagramas equivalentes a los del margen izquierdo de la Figura 6 se presentan con respecto a los datos ajustados de devoluciones en el margen derecho de la figura. Estos diagramas parecen ser bastante similares a los datos no ajustados correspondientes, diferenciándose principalmente por la cantidad de peces. Aparece un ejemplo notable en el recuadro de la Dirección 6 de los peces liberados en el área de Acapulco en 1969; en este caso se ajustó una devolución individual a 34 devoluciones en octubre debido a que el esfuerzo fue bajo en el estrato de área de 5 grados y mes. Son interesantes las diferencias en los direcciones de desplazamiento de las devoluciones no ajustadas y ajustadas del mes de febrero de peces liberados en el área de Acapulco en 1969. Respecto a los datos no ajustados, 7 de las recapturas se obtuvieron al sudeste (Direcciones 2 y 3) y 36 al noroeste (Direcciones 6 y 7); con relación a los datos ajustados 24 de las recapturas se lograron al sudeste y 12 al noroeste. Esto indica que los peces liberados en el área de Acapulco en 1969 tienen la tendencia a distribuirse más hacia el sudeste que al noroeste (*e.d.* en el área de Manzanillo o cerca de allí) en febrero 1970.

Las medias cuadradas de los coeficientes de dispersión por meses de recaptura, según fueron calculadas por los datos de devolución no ajustados, se presentan en el margen izquierdo de la Figura 7. Los puntos se grafican solamente para los meses que incluyen por lo menos cinco devoluciones. Las cifras cerca de los puntos indican las cantidades de devoluciones en cada mes. Los valores de $a_{j\cdot}^2$ son superiores en los experimentos iniciados en 1969 ya que el esfuerzo se esparció en 1970 a un área mucho más grande, lo que dió como resultado que las recapturas se encontraron también diseminadas en un área mucho mayor. Las tendencias son muy similares a aquellas de los promedios de las distancias cuadradas de desplazamiento (Figura 4). Sin embargo, no existe la tendencia de que los valores de $a_{j\cdot}^2$ aumenten con el tiempo, posiblemente con la excepción de aquellos peces liberados en el área de Acapulco en 1969. Los valores en febrero de $a_{j\cdot}^2$ son bajos para los peces liberados en el área de Manzanillo en 1969 y altos en ese año respecto a los peces liberados en las áreas de Acapulco y los 10°N-100°W, ésto debido probablemente a la gran cantidad de esfuerzo de pesca ejercido en el área de Manzanillo y a la poca cantidad ejercida en el área de Acapulco en febrero 1970.

Los diagramas equivalentes a los del margen izquierdo de la Figura 7 se presentan en el margen derecho de esa figura respecto a los datos ajustados de recaptura. Los resultados son bastante similares a los obtenidos por los datos no ajustados, siendo la diferencia principal que no parece que exista una tendencia progresiva para los peces liberados en el área de Acapulco en 1969. Por la razón dada en la discusión del método de Skellam, es lógico suponer que el alto esfuerzo ejercido en el área de Manzanillo durante febrero de 1970 se debió por lo menos en parte a una afluencia de peces de las áreas de Acapulco y los 10°N-100°W.

Método variancia-covariancia

Se usan en este método las coordenadas cartesianas, en lugar de las coordenadas polares empleadas en el método de Jones. Se supone que cada pez ha sido liberado en el punto (0,0), y la localidad de recaptura se expresa como la distancia este o oeste (X) y norte o sur (Y) de este punto. La matriz variancia-covariancia de las recapturas en el mes j de un grupo de liberaciones se calcula mediante

$$\begin{bmatrix} \sum^{n_j}(X_j-\overline{X}_j)^2/n_j-1 & \sum^{n_j}(X_j-\overline{X}_j)\;(Y_j-\overline{Y}_j)/n_j-1 \\ \sum^{n_j}(X_j-\overline{X}_j)\;(Y_j-\overline{Y}_j)/n_j-1 & \sum^{n_j}(Y_j-\overline{Y}_j)^2/n_j-1 \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \qquad (13)$$

donde

n_j = cantidad de devoluciones durante el mes j,

$\overline{X}_j = \sum^{n_j} X_j/n_j$ y

$\overline{Y}_j = \sum^{n_j} Y_j/n_j$.

El determinante de la matriz variancia-covariancia se calcula mediante

$$(a_{11} \times \mathrm{a}_{22}) - (a_{12} \times a_{21}) \qquad (14)$$

y el coeficiente de correlación por

$$[(a_{12} \times a_{21})/(a_{11} \times a_{22})]^{1/2} \; . \qquad (15)$$

Es evidente que si el desplazamiento de un grupo de peces fue aproximadamente en un ángulo de 45 grados con relación a la abcisa a la ordenada, o sea nordeste, sudeste, sudoeste o noroeste (o en dos direcciones opuestas), sería más probable que el coeficiente de correlación sea significativo que si lo fuera aproximadamente a lo largo de uno de los ejes, o sea norte y/o sur o este y/o oeste. Con el fin de remediar este sesgo se giraron los ejes, empleando un método concebido por el Dr. Robert C. Francis. La abcisa y la ordenada transformadas fueron aquellos ejes a través del origen que estaban en angulos de 45 grados respecto a la dirección de máxima variabilidad en el sistema original de las coordenadas cartesianas. Esa dirección fue determinada al computar el primer vector característico de la matriz original variancia-covariancia. Este procedimiento pone al máximo los coeficientes de correlación.

Se calcula la matriz ajustada variancia-covariancia mediante

$$\begin{bmatrix} \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij} - \overline{X}_{ij})^2/n_j - 1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) & \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij} - \overline{X}_{ij})\ (Y_{ij} - \overline{Y}_{ij})/n_j - 1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \\ \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (X_{ij} - \overline{X}_{ij})\ (Y_{ij} - \overline{Y}_{ij})/n_j - 1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) & \left(\sum_{i}^{n_j} \frac{1}{f_{ij}} (Y_{ij} - \overline{Y}_{ij})^2/n_j - 1\right) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \end{bmatrix} \tag{16}$$

donde

$$\overline{X}_{ij} = \sum_{i}^{n_j} (X_{ij}/f_{ij}) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \quad \text{y}$$

$$\overline{Y}_{ij} = \sum_{i}^{n_j} (Y_{ij}/f_{ij}) \Big/ \sum_{i}^{n_j} (1/f_{ij}) \ .$$

El determinante de la matriz variancia-covariancia y el coeficiente de correlación evidentemente se encuentran estrechamente relacionados ya que el primero se obtiene al substraer un número más pequeño de uno más grande y el segundo se obtiene al dividir el mismo número menor por el mismo número mayor y luego se saca la raíz cuadrada del cociente. El determinante de la matriz variancia-covariancia es un índice de la dispersión de los peces; cuando las distancias de los peces son grandes la una de la otra el determinante es grande. Por lo consiguiente es muy similar a los valores $a_{j\cdot}^2$ del método de Jones. El coeficiente de correlación se aproxima a 0 cuando el desplazamiento es aleatorio y se aproxima a 1 cuando el desplazamiento es solamente en una dirección o en dos direcciones opuestas.

El método variancia-covariancia se basa en probabilidades, así que cuando se ajustan los datos ésto anula las estimaciones del determinante de la matriz variancia-covariancia y del coeficiente de correlación. No obstante, estas estimaciones se presentan en las figuras para compararlas con aquellas obtenidas por los datos no ajustados.

Los promedios de las localidades de recaptura por meses de recaptura, según se calcula de los datos de devolución no ajustados, se presentan en el margen izquierdo de la Figura 8. Los puntos se grafican solo respecto a los meses que incluyen por lo menos cinco devoluciones. Las cifras cerca de los puntos indican los meses de recaptura (1 = enero, 2 = febrero, etc.).

De nuevo es evidente que los peces liberados en el área de Acapulco en 1960 fueron recapturados en su mayoría al noroeste y que los liberados en ese año en el área de Manzanillo fueron recapturados en su mayoría al sudeste. Es además aparente que los peces liberados en las áreas de Manzanillo y Acapulco en 1969 fueron recapturados en su mayor parte al sudeste, mientras que los liberados mar adentro fueron recapturados en su mayoría al este y nordeste. Sin embargo, los peces liberados en el área de Acapulco en 1969 aparecieron en su mayoría hacia el noroeste del área de liberación en febrero 1970, coincidiendo con la gran cantidad de esfuerzo de pesca en el área de Manzanillo durante ese mes. Asímismo, los peces liberados en 1969 en las áreas de los 10°N-100°W y 10°N-108°W aparecieron más al norte del área de liberación en febrero que en cualquiera de los otros meses de 1970.

Los diagramas equivalentes a los del margen izquierdo de la Figura 8 se presentan para los datos ajustados de devolución en el margen derecho de la figura. Los diagramas en los márgenes izquierdo y derecho de esta figura se diferencian más los unos de los otros que los de los márgenes izquierdo y derecho de cualquiera otra figura. Parece que los peces liberados en 1969 en el área de Acapulco no emigraron en grandes cantidades al área de Manzanillo a principios de febrero de 1970; así que la captura total fue grande en esa área durante ese mes debido a que los peces que ya estaban allí fueron más vulnerables a la pesca o a causa de que hubo un ingreso de peces de grupos distintos a los que pertenecían los peces liberados en el área de Acapulco en 1969. Lo mismo puede aplicarse a los peces liberados en 1969 a los 10°N-100°W; su desplazamiento a principios de febrero 1970 fue principalmente hacia el este.

Los determinantes no ajustados y ajustados de las matricies variancia-covariancia por meses de recaptura se presentan en los márgenes izquierdo y derecho de la Figura 9. Los resultados son similares a los presentados en las Figuras 4 y 7, siendo la disimilitud principal que las diferencias entre los seis grupos de liberaciones son mayores respecto a las extensiones (rangos) de las distribuciones de los determinantes que para las extensiones de las distribuciones de los parámetros en las otras dos figuras. Se esperaba que los resultados fueran particularmente similares a los de la Figura 7, pero indican una tendencia progresiva con el tiempo correspondiente a los peces liberados en 1969 en el área de Acapulco, que se parece más a la tendencia indicada en la Figura 4 que a la de la Figura 7.

Los coeficientes de correlación no ajustados y ajustados por meses de recaptura se presentan en los márgenes izquierdo y derecho de la Figura 10. Los resultados son similares a los indicados en las Figuras 4, 7 y 9, especialmente la Figura 7. Solo dos coeficientes de correlación no ajustados en meses con más de seis devoluciones no fueron significativos al nivel del 5 por ciento; éstos fueron los coeficientes de correlación del área de Manzanillo en enero 1970 (g. l. = 17, r = 0.217) y el área de los 10°N-100°W en enero 1970 (g. l. = 27, $r = 0.356$). Sin embargo, los coeficientes de correlación ajustados fueron significativos para ambas áreas ($r = 0.669$, $P < 0.01$ para el primero y $r = 0.649$, $P < 0.01$ para el último). Solo hubo un coeficiente de correlación no significativo para los datos ajustados en un mes con más de seis devoluciones; en este caso fue para el área de Acapulco en marzo 1970 (g. l. = 67, $r = 0.217$).

Talla de los peces y efecto de la talla sobre la dirección de desplazamiento

Sería conveniente comparar la distribución de tallas al momento de liberación de los peces marcados que fueron devueltos con relación a la distribución de las frecuencias de talla de los peces capturados en las mismas áreas al mismo tiempo para ver si los primeros representan estos últimos. Además, es conveniente comparar las direcciones de desplazamiento de los peces de diferentes tallas.

Los datos sobre la distribución de las frecuencias de talla de los peces en las capturas se obtienen rutinariamente por mediciones de muestras de 50 peces poco tiempo después de que han sido desembarcados en los enlatadoras (Hennemuth, 1957). Los datos apropiados se presentan en la Figura 11. Los datos de las frecuencias de talla en 1960 del área de Acapulco consisten en nueve muestras de peces capturados por clípers en esa área en marzo y abril de 1960. Los del área de Manzanillo en 1960 consisten de una muestra de peces capturados por un clíper en esa área en agosto de 1960; estos datos no se presentan en la figura porque los peces marcados y liberados en agosto de 1960 no fueron medidos. Los datos de las frecuencias de talla en 1969 consisten en una muestra de peces descargados por el barco usado para el marcado. (No se obtuvieron otras muestras porque, debido a las regulaciones mencionadas antes, no había otros barcos pescando en el área durante el último trimestre de 1969). Esta muestra incluía una mezcla de peces capturados en las áreas de Acapulco y los 10°N-108°W. Estaba sesgada debido a que se sacaron los peces de los capturados para el marcado y, según se demostrará más adelante, no se seleccionaron porciones iguales de peces de todas las tallas con este propósito.

Los datos sobre la distribución de tallas a tiempo de liberación de los peces marcados que fueron devueltos se presentan también en la Figura 11.

La captura en 1960 en el área de Acapulco parece que consistió en tres grupos de peces, aunque la mayoría de los peces marcados que fueron devueltos parece que pertenecían al grupo del medio. Por lo consiguiente los datos presentados en este informe pueden representar solo las migraciones de los peces del grupo del medio.

Los peces marcados en el área de Manzanillo en 1960 tenían probablemente de unos 50 a 60 cm de longitud (Fink y Bayliff, 1970: 208). Los 50 peces de la muestra correspondiente a la captura tenían en su mayoría de

54 a 62 cm de longitud, así que los peces marcados representaban probablemente bastante bien aquellos capturados en esa área durante ese mes.

La muestra sesgada de la captura en 1969 de las áreas de Acapulco y los 10°N-108°W indica dos grupos de peces, uno con peces de una talla inferior a 100 cm y el otro con peces de más de 110 cm. La gran mayoría de los peces marcados que fueron recapturados tenían menos de 100 cm de longitud cuando fueron liberados. Así que en este caso los datos presentados en este informe pueden representar solo las migraciones de los peces más pequeños.

Los peces del grupo más grande, aquellos liberados en el área de Acapulco en 1969, fueron seleccionados para comparar las direcciones de desplazamiento de los peces de diferentes tallas. Se preparó un gráfico de las frecuencias de talla de los peces marcados y liberados en esta área, y basados en ésto los peces que fueron devueltos se dividieron en las siguientes categorías: pequeños 42-71 cm (62 peces); medianos, 72-93 cm (294 peces); grandes, 94-126 cm (18 peces); desconocidos (5 peces). Un examen preliminar de los datos indicó que los peces pequeños tienden a migrar más hacia el noroeste que al sudeste, mientras sucede lo contrario con los peces medianos y grandes. Se observó que las porciones de los peces pequeños y medianos difieren entre las caladas realizadas en diferentes localidades en el área de Acapulco, así que las diferencias en dirección de desplazamiento pueden ser debidas a las diferencias en la localidad de liberación en lugar de a las diferencias de talla de los peces. Con el fin de examinar ésto se dividieron los datos entre cinco localidades de liberación, tres direcciones de desplazamiento, sudeste (Direcciones 2 y 3), sudoeste (Direcciones 4 y 5) y noroeste (Direcciones 6 y 7) y dos tallas, pequeña y mediana. Los peces se habían liberado en siete áreas de 1 grado, pero se combinaron los datos de dos de ellas con las dos áreas más cercanas de 1 grado para evitar compartimentos vacíos. Los datos de los peces que se desplazaron en las Direcciones 0 y 1 y los de los peces grandes no se consideraron ya que había muy pocos en esas categorías. Los resultados de las pruebas de *G* (Sokal y Rohlf, 1969: 601-607) son los siguientes:

Hipótesis	Grados de libertad	*G*	Probabilidad
Independencia de localidad × talla	6	34.046	< 0.01
Independencia de localidad × dirección	8	33.056	< 0.01
Independencia de talla × dirección	2	20.936	< 0.01
Interacción de localidad × talla × dirección	8	2.798	> 0.05
Total	22	91.286	

La interacción no significativa indica ya sea que la diferencia en las direcciones de desplazamiento de los peces pequeños y medianos fue causada por diferencias en las porciones de los peces pequeños y medianos liberados en las diferentes localidades o que la diferencia en direcciones de desplazamiento de los peces liberados en las diferentes localidades fue causada por diferencias en las porciones de los peces pequeños y medianos en esas localidades. El examen de los datos revela que este último es el caso; por lo consiguiente los peces pequeños tienden a migrar más hacia el noroeste y los peces medianos más hacia el sudeste.

Una prueba de contingencia del ji-cuadrado indica que no hay diferencia en las direcciones de desplazamiento de los peces medianos y grandes ($\chi^2 = 0.533$, g. l. $= 2$, $P > 0.05$). Sin embargo, la cantidad devuelta de peces grandes fue limitada, y la mayoría de éstos fueron más pequeños que los grandes peces de la muestra (Figura 11). Si se hubieran marcado y devuelto porciones iguales de peces capturados de todas las tallas, probablemente hubiera habido más desplazamiento hacia el sudeste y menos al noroeste, pero no se tiene seguridad sobre ésto debido a que se liberaron tan pocos peces marcados de una talla superior a los 100 cm.

SUMARIO Y CONCLUSIONES

El método de mapas, el de Jones y el de la variancia-covariancia son todos útiles para estudiar las migraciones de aleta amarilla, y cada uno presenta información que complementa la presentada por los otros. El método de Skellam, conforme se emplea en este informe, es menos útil.

Los desplazamientos de los peces marcados y liberados en 1960 parecen que hubieran sido fuertemente orientados, pero se indicó que esto probablemente fue causado principalmente por la distribución del esfuerzo de pesca. El esfuerzo se distribuyó más extensamente en 1970, y el desplazamiento de los peces parece que fue menos orientado. Los coeficientes de correlación derivados del método variancia-covariancia indicaron, sin embargo, que de ninguna manera fueron aleatorios.

Una de los cuestiones más interesantes es que si una porción principal de los peces marcados y liberados en las áreas de Acapulco y los 10°N-100°W en 1969 migraron sí o no al noroeste al área de Manzanillo a principios de febrero 1970. Si se hubieran analizado los datos solamente por el método de Skellam se hubiera determinado que este era el caso. Sin embargo, al emplear el método de los mapas, el de Jones y el de la variancia-covariancia se demostró que cuando se ajustan los datos el desplazamiento al área de Manzanillo no tuvo relativamente importancia. Un análisis del desplazamiento por talla indicó que los peces pequeños tienden a desplazarse al noroeste y los medianos y grandes tienden a desplazarse al sudeste.

Sería conveniente comparar los datos de los peces marcados liberados en las mismas áreas durante los mismos meses en otros años para determinar el grado de variación de las migraciones en diferentes años. Estos experimentos fueron iniciados en pequeña escala en 1970, 1971, 1972 y 1973, y las comparaciones se harán eventualmente. Sería además conveniente estudiar las migraciones de los peces marcados liberados en otras áreas, especialmente frente a la América Central y fuera del ARCAA. Los peces marcados fueron liberados en estas áreas en 1970 y 1971, pero en una escala muy inferior a la necesaria. Los experimentos frente a la América Central se iniciaron durante abril, mayo y junio, pero deben iniciarse también durante octubre, noviembre o diciembre para obtener ventaja del período máximo de pesca en esa área durante enero a mayo. Finalmente, sería conveniente marcar y liberar más peces grandes. Desafortunadamente, sin embargo, estos peces son tan difíciles de manipulear que ésto sería casi imposible de realizar.

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7405

A Simple Apparatus for Metering Volatile Liquids into Water

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BENVILLE, P. E. JR., AND S. KORN. 1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31: 367–368.

A metering device was developed to introduce benzene, toluene, xylene, and 1,2,4 trimethylbenzene vapors into water using air as a carrier gas. Setting the carrier gas flows for the respective aromatics at 10, 25, 120, and 500 cm^3/min for 2 h resulted in concentrations of 8.2, 13.0, 12.0, and 7.2 µl/liter, respectively, in 4 liters of water. The aromatic concentrations were maintained in a static system by bubbling air through the water, and in a continuous flow system by replenishing the water. In static systems the respective aromatic concentrations were maintained for 4 days within the ranges of 13–14, 5.1–7.0, 0.40–0.50, and 0.018–0.028 µl/liter by bubbling the aromatics into the water at 5 cm^3/min and independently aerating the water at 100 cm^3/min. In a 14-day continuous flow system benzene concentrations ranged from 2.1–2.8 µl/liter when benzene was bubbling at 23 cm^3/min and water was flowing at 1.8 liters/min.

BENVILLE, P. E. JR., AND S. KORN. 1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31: 367–368.

Nous avons mis au point un compteur pour mesurer les vapeurs de benzène, toluène, xylène et 1,2,4 triméthylbenzène introduites dans l'eau, utilisant l'air comme gaz porteur. Le réglage des débits du gaz porteur, pour les aromatiques respectifs, à 10, 25, 120 et 500 cm^3/min pendant 2 h donne des concentrations de 8.2, 13.0, 12.0 et 7.2 µl/litre, respectivement, dans 4 litres d'eau. Les concentrations d'aromatiques sont maintenues en régime statique par barbotage d'air dans l'eau ou en régime à flot continu par renouvellement de l'eau. En régime statique, les concentrations d'aromatiques respectifs ont été maintenues pendant 4 jours dans les limites de 13–14, 5.1–7.0, 0.40–0.50 et 0.018–0.028 µl/litre en barbotant les aromatiques dans l'eau au taux de 5 cm^3/min et en aérant l'eau indépendamment au taux de 100 cm^3/min. En régime à flot continu pendant 14 jours, les concentrations de benzène ont varié de 2.1 à 2.8 µl/litre avec barbotage de benzène au taux de 23 cm^3/min et débit d'eau de 1.8 litres/min.

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THIS note describes a device that vaporizes liquids, meters their vapors into water, and maintains their concentration in water for extended periods. The liquids that are currently being used in our acute and chronic studies on fish are benzene, toluene, xylene, and 1,2,4, trimethylbenzene. We determined that these aromatics are relatively insoluble in freshwater (1993, 401, 221, and 104 µl/liter, respectively) and volatilize rapidly from water. We found that 46–56% of these aromatics volatilized within 24 h from a 4-liter solution maintained at 20 C. Aerating the solution at 20 cm^3/min increased the loss to 97–100%. Other metering apparatuses (American Public Health Association 1971; Mount and Warner 1965; Mount and Brungs 1967) were not suitable for metering these compounds because of the low solubilities, high volatilities, and high dosages necessary to produce toxic effects in fish. Our system avoids these difficulties by using air as a carrier to introduce the volatile compound into water. Another air source or water flow is used to maintain a stable concentration of the compound in water.

The metering systems — The static metering system is composed of two independent air sources (Fig. 1). One air source vaporizes the volatile liquid in the gas washing bottle and transports the vapor into the water. The vapor dissolves in the water and accumulates if there is no second air stream until saturation is reached. An accumulation experiment was conducted with four aromatics by aerating each aromatic into 4 liters of water at 20 C, one vapor flow rate being used for each aromatic. The concentrations of these aromatics were determined at three time intervals by extracting a 100-ml water sample twice with 10 ml of TF Freon (trifluorotrichloroethane). An aliquot of the 20-ml extract was injected into a gas chromatograph equipped with a 6-ft column. The column was

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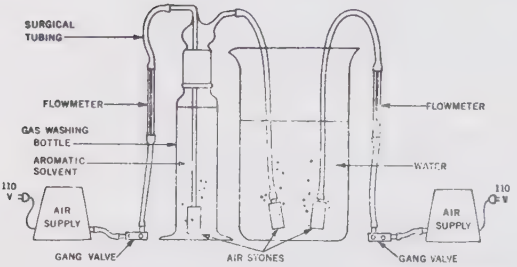

FIG. 1. Components of the static metering system.

packed with 5% Bentone-34 and 10% didecylphthalate on 80/100 mesh chromosorb PAW. The four aromatics accumulated rapidly in water (µl/liter):

Time (h)	0.5	1	2
Benzene (10)[a]	1.4	3.5	8.2
Toluene (25)	3.0	6.2	13
Xylene (120)	3.8	6.6	12
1,2,4 Trimethylbenzene (500)	3.7	5.8	7.2

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[a] Vapor flow (cm^3/min).

Low concentrations of the aromatics in water are maintained by utilizing a second air source to limit accumulation of the dissolved vapors in water. At specific vapor and air flow settings an equilibrium is reached between the amounts of vapor dissolving and dissipating from the water. A 4-day equilibrium study was conducted with the four aromatics to determine the daily fluctuations in concentration. The air flows were set at 5 cm^3/min for vaporizing the aromatics and at 100 cm/^{3}min for aerating the water. For water samples taken daily after 24 h the concentrations (µl/liter) were:

Day	1	2	3	4
Benzene	14	13	14	13
Toluene	5.1	7.0	6.7	7.0
Xylene	0.50	0.41	0.43	0.40
1,2,4 Trimethylbenzene	0.028	0.024	0.024	0.018

In a continuous flow system the second air source is replaced by a flowing water source. With a continuous flow system that we had in operation for 2 wk, benzene concentrations were maintained at 2.1–2.8 µl/liter in 65 liters of water at 12 C. The vapor flow was 23 cm^3/min, the water flow 1.8 liters/min.

In both the static and flowing systems the air flow is observed on a flowmeter and controlled by a gas or gang valve. To maintain a constant air flow we tried three different air sources. In order of reliability, these are an air cylinder with a two stage regulator, an oilless air compressor with reservoir, and an aquarium air pump.

We found variations in the dissolved aromatic concentrations between some systems even though the flow rates were identical. Factors that caused the most variation in the concentrations were coarseness of the air stone or fritted disc, volume of the water, and shape of the aquaria. Also, temperature and salinity would be expected to affect the concentrations. Poon (1972) has discussed in depth the various factors influencing bubble aeration. Therefore, each system must be calibrated and furthermore should be monitored periodically as a quality control measure.

Advantages of the technique — Fish undergo many stresses during toxicity experiments that are not necessarily related to the compound being tested. Some of these stresses (such as decreasing oxygen concentrations and increasing carbon dioxide, ammonia, and other volatile wastes) may produce additive effects which bias the results. These stresses are reduced in our technique by aeration.

Some and perhaps most toxicants metered into aquaria are sufficiently insoluble in water to necessitate using a solubilizing agent with the toxicant. The solubilizing agent has a toxic effect on fish that can result in synergistic or antagonistic biases in the toxicity data. Our technique disperses the toxicant into the aquaria without a second compound.

The toxicants are replenished instantaneously in the solution, thereby maintaining a constant toxicant concentration. Any toxicant concentration in water below the saturation level can be achieved by changing one or both of the flow rate ratios, i.e. toxicant aeration to aquarium aeration and toxicant aeration to water flow. Thorough mixing of the toxicant is achieved by aeration. The toxicant is vaporized before it goes into solution, reducing the formation of colloidal particles and precipitates.

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7406

Heat Exchange Between Ocean and Atmosphere in the Eastern North Pacific for 1961-71

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ABSTRACT

Summaries of large-scale heat exchange between ocean and atmosphere in the eastern North Pacific Ocean are presented for the period 1961 through 1971. The summaries are based on computations made from synoptic marine radio weather reports and include 1) monthly values of total heat exchange and departures from a long-term mean; 2) long-term monthly mean values of the total heat exchange, incoming solar radiation, effective back radiation, and evaporative and sensible heat transfer; and 3) annual cycles of total heat exchange for selected areas.

Outstanding spatial and temporal features of the heat exchange values are discussed. However, little detail is given since this is a summary report, and readers can draw their own conclusions depending upon the intended use of the charts.

Comparisons are also made between the total heat exchange values and those given in two other reports. Discrepancies between values given in this report and those published in the other reports are attributed to differences in the empirical equations used to make the heat exchange computations, differences in data processing techniques, differences in the observed data used in the computations due to different methods of acquisition, and the possibility of ocean climate changes.

INTRODUCTION

The ocean's thermal structure is an important environmental variable that affects the distribution and abundance of marine fish populations (Sette, 1961; Uda, 1957, 1961). As part of a fisheries oceanography research program directed towards fisheries prediction, ocean temperature conditions and the air-sea interaction processes which are most often responsible for changes in this structure have been monitored in the eastern North Pacific since 1960. These data have been used to describe the interaction of ocean and atmosphere (Clark, 1972; Namias, 1969, 1971) in the eastern North Pacific and to identify and attempt to understand those ocean features that are important determinants of tuna distribution (Johnson, 1962; Flittner, 1970). They are also being used to evaluate the role of changing ocean conditions on other fish populations.

This report is a contribution to the MARMAP program of the National Marine Fisheries Service and presents summaries for use by fishery and other marine scientists of the derived heat exchange between ocean and atmosphere in the eastern North Pacific Ocean bounded by lat. 20° and 60°N and long. 115°W and 180° for the period 1961-71. The summaries were computed by 5° latitude-longitude quadrangles and are presented on charts of 1) the monthly values of total heat exchange and differences from the long-term mean; 2) the long-term monthly means of the total heat exchange, incoming solar radiation, effective back radiation, and evaporative and sensible heat transfer; and 3) the annual cycles of total heat exchange in selected areas.

Since air-sea interaction processes cannot, in general, be measured directly except for solar radiation, for which there are very limited measurements over the oceans, quantitative evaluation of these processes depends upon computations based on empirically derived formulas. Because these formulas are still the subject of extensive research, the heat exchange computations should be considered only as relative indices of the magnitude of the heat flux across the air-sea interface. However, we believe that the computations represented by the charts in this report can be used to evaluate large-scale features and to show year-to-year and month-to-month variations of this heat flux.

SOURCE AND DISTRIBUTION OF THE DATA

The source of data used in preparing the charts in this report is the synoptic marine radio weather report made by ships at sea. Cooperating American and foreign-flag vessels make, record, and transmit the standard marine weather observations according to established procedures set up by the World Meteorological Organization (WMO). Observations taken at 0000, 0600, 1200, and 1800 Greenwich Mean Time daily are transmitted to designated commercial and government radio stations around the world.

Between 8,000 to 10,000 synoptic marine weather observations from the eastern North Pacific are processed by computer each month at the National Marine Fisheries Service La Jolla Laboratory, and several summaries are compiled depending on their intended use. For a more detailed description of how the observations are received and processed, see Johnson, Flittner, and Cline (1965). Although specific program details have been changed, the present processing methods are essentially the same as those described in that publication.

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Because the data are compiled from merchant and fishing vessel marine weather reports, the spatial and temporal distributions of observations over the ocean are irregular. Observations are most numerous in the major shipping lanes from San Francisco to Hawaii, from San Francisco to Japan, from Panama to San Diego, Los Angeles, and San Francisco, and from Seattle to Japan. Shipping lanes of secondary importance are from San Diego to Hawaii and Panama to Hawaii.

The average number of marine synoptic observations taken per month over the period 1961-71 by 5° quadrangles for the winter and summer seasons is shown in Figures 1a and 1b, respectively. The density of observations is shown in class intervals of 50 as indicated on the charts. Compilations made for the spring and fall seasons show the density distribution for spring similar to that of winter and the density distribution for fall similar to that of summer.

In all seasons, most observations are taken along the shipping lane between San Francisco and Hawaii and the coastal route from Panama to U.S. west coast ports. The least number of observations are taken northwest of Hawaii and between lat. 25° and 30°N during the summer season. The main difference between the winter and summer distributions is the southward shift of greatest observation density west of long. 145°W from the great circle route to Japan during summer to between lat. 30° and 35°N during winter.

INITIAL DATA PROCESSING AND CHART PREPARATION

Marine Environmental Variable and Heat Exchange Summaries

An intermediate step between reception of the synoptic marine data and preparation of the charts presented in this report is the compilation by 5° quadrangles of monthly mean marine synoptic variables

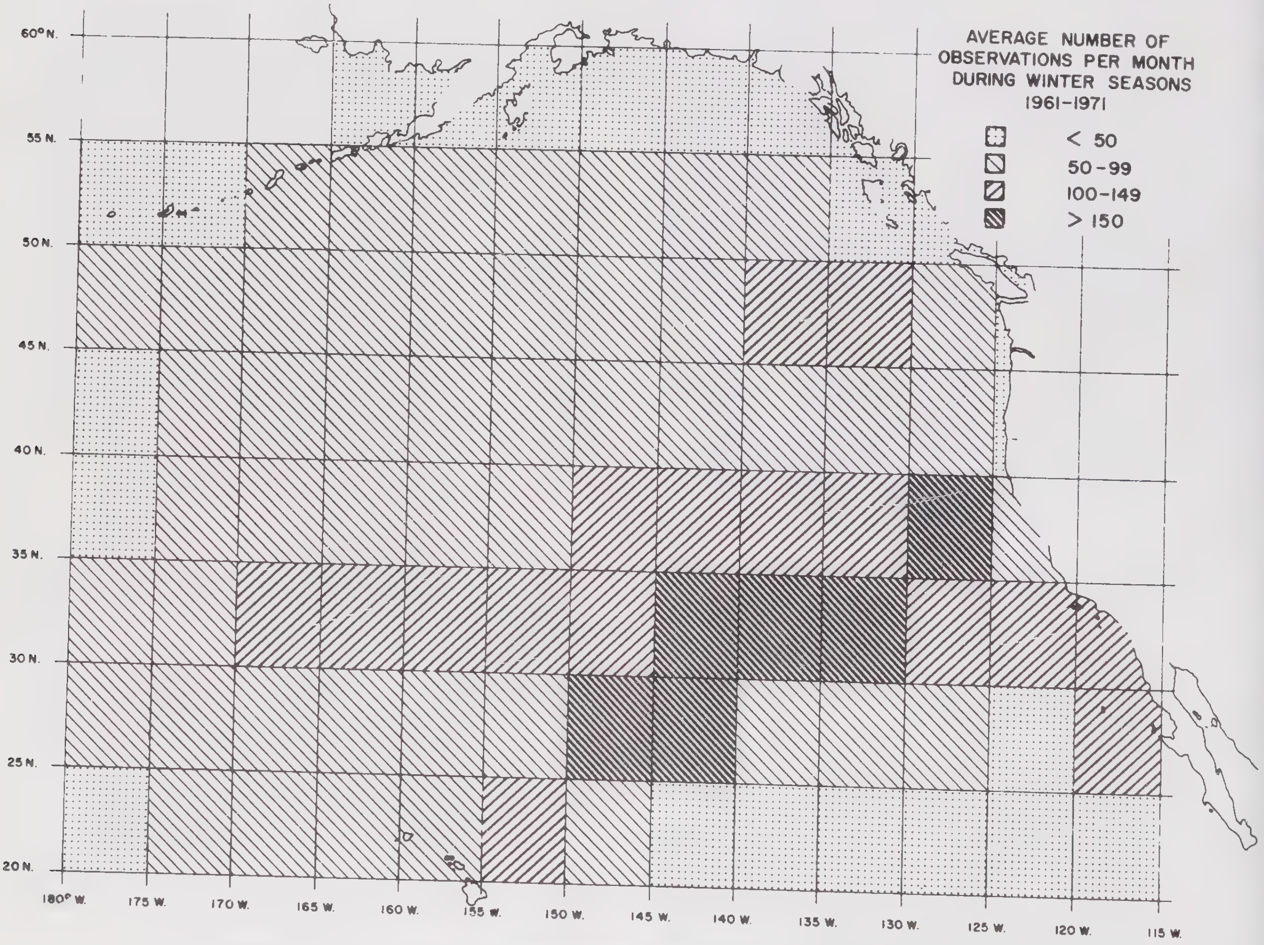

Figure 1a.—Average number of observations per month during winter seasons for 1961-71.

and heat exchange values that are computed from the variables. The initial output format consists of a deck of computer cards which are sorted and reprocessed in order to display the values in a geographic format. Each of the variables and heat exchange terms (described below) is printed in this format after three summaries have been made: 1) long-term mean monthly values computed over the years 1961-71; 2) monthly mean values computed for a given month and year; and 3) deviations of a value for a given month and year from the long-term monthly mean, i.e., anomaly values.

Heat Exchange Computations

For a given area and time period, the equation for the energy exchange at the air-sea interface is $Q_t = Q_{io} - Q_r + Q_b + Q_e + Q_s$. Energy exchange calculations presented here do not take into account changes in heat brought about by advection.

Q_{io}, the incoming solar radiation corrected for cloud cover (cal/cm²/day), is determined from the following equation proposed by Berliand (1960):

$$Q_{io} = \text{(Berliand table)}\,(1 - aC - bC^2)$$

where $C =$ cloudiness in tenths;
$b =$ 0.38; and
$a =$ a function of latitude.

Berliand's table, which lists values by month and latitude of incoming solar radiation with a clear sky, and values of "a" are given in Johnson et al. (1965).

Of the incoming radiation corrected for the screening effects of cloud cover, some is reflected at the sea surface. The amount reflected depends on the latitude and time of year and is computed from

$$Q_r = Q_{io} \bullet r$$

where r = percentage of radiation reflected given in a table by Budyko (1956). The percentage varies from about 6% in low latitudes to more than 20% in high latitudes in winter. In preparing the charts, Q_{io} and Q_r were combined in a single term Q_i, the incoming radiation corrected for cloud cover and reflection, defined by $Q_i = Q_{io} - Q_r$.

Effective back radiation, Q_b (cal/cm²/day), is the difference between long-wave radiation from the sea surface and long-wave radiation from the atmosphere. The following semiempirical equation proposed by

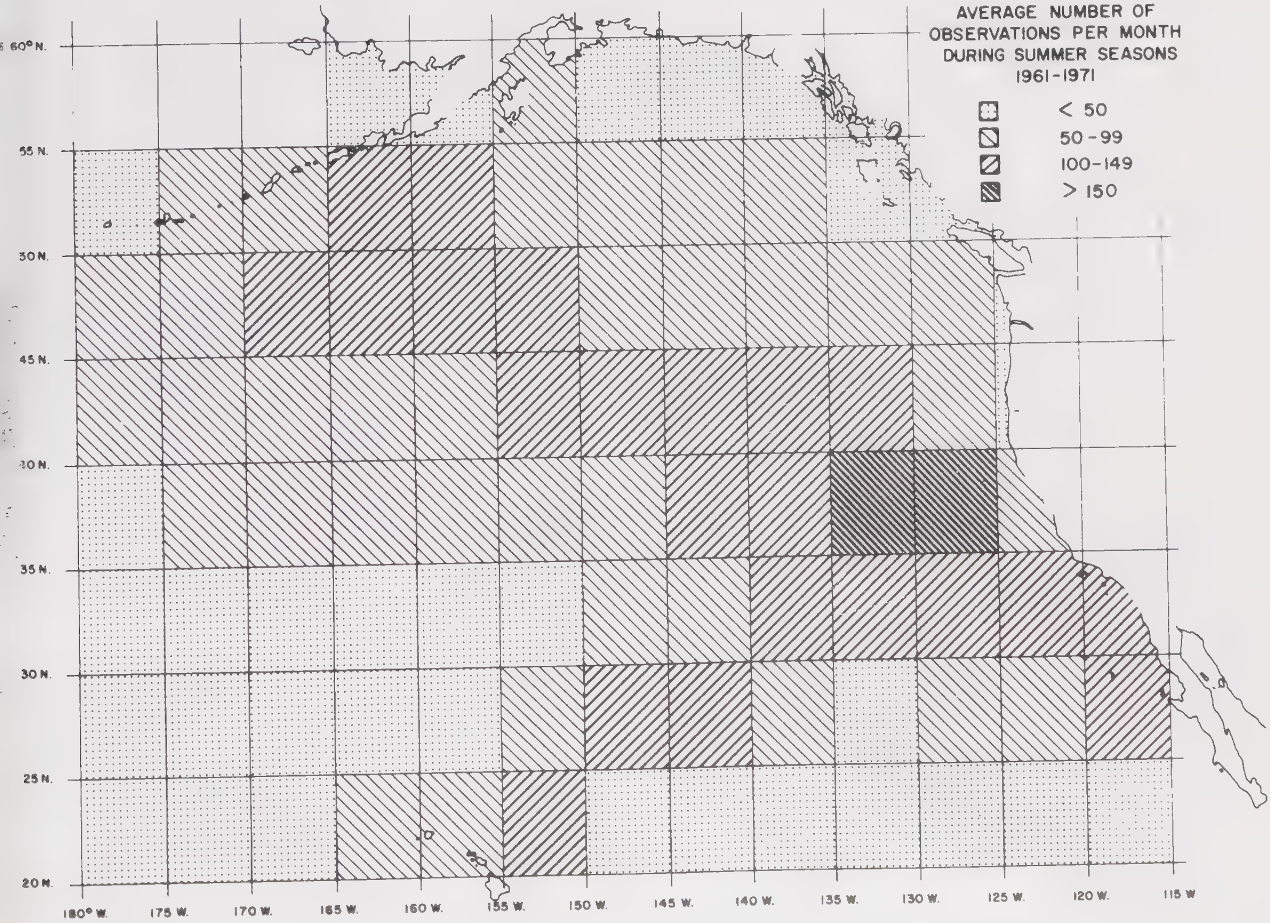

Figure 1b.—Average number of observations per month during summer seasons for 1961-71.

Berliand and Berliand (1952) has been used in this study:

$$Q_b = -\left[s\sigma(\theta_s)^4(0.39 - 0.050\sqrt{e_a})(1 - kC^2) + 4s\sigma\theta_s^3(\theta_s - \theta_a) \right]$$

where $s =$ 0.97 (the ratio of the radiation of the sea surface to a black body);
$\theta_s =$ absolute sea surface temperature (°K);
$\theta_a =$ absolute air temperature (°K);
$\sigma =$ 1.175×10^{-7} (the Stefan-Boltzmann constant);
$e_a =$ vapor pressure (mb);
$k =$ a function of latitude (values given in Johnson et al., 1965);
$C =$ cloudiness in tenths of celestial dome covered.

Additional energy enters or leaves the sea surface as evaporation (Q_e) and sensible heat (Q_s). Evaporation depends upon 1) the velocity of the wind and the vapor pressure difference between the sea surface and air above it, and 2) a coefficient of proportionality. The coefficient of proportionality used in our computations is given by Tabata (1958):

$$Q_e = -4.70\,(e_s - e_a)W$$

where $e_s =$ saturation vapor pressure at temperature of sea surface (mb);
$e_a =$ vapor pressure of air (mb); and
$W =$ wind speed (m/sec).

Bowen (1926) established the relation between evaporation and the heat conduction at a water surface. The equation used here for sensible heat loss by the ocean is derived from the relation found by Bowen:

$$Q_s = -3(T_s - T_a)W$$

where $T_s =$ sea temperature (°C);
$T_a =$ air temperature (°C); and
$W =$ wind speed (m/sec).

Preparation of the Heat Exchange Charts

Preparation of the charts presented in this report began by transferring the heat exchange values from computer printouts to a map of the eastern North Pacific and then contouring them by hand. In drawing the isolines, subjective smoothing was used, and, therefore, the lines do not always conform to the numbers as printed. This technique was used to eliminate the influence of values that could be an order of magnitude different from surrounding ones, a problem that is usually due to observation errors.

Caution should be exercised in interpreting the individual energy exchange values in regions having limited observational coverage (see Fig. 1a, 1b). Small errors in observation and transmission can cause large errors in some of the computations. In quadrangles having few observations, considerable bias can be introduced by the relative positions of the reporting ships and their timing with respect to the calendar month. All computations presented assume the data centroid to be at the center of each respective quadrangle and for the middle of the month. Energy exchange calculations were not made for 5° quadrangles having fewer than five observations per month.

CHARTS PREPARED FROM THE HEAT EXCHANGE COMPUTATIONS

Monthly Average and Anomaly Charts

Monthly averages and anomalies of the total (net) heat exchange, Q_t, across the air-sea interface are shown for each month of the 11-yr period, 1961-71, in Part 1 of the chart section. A detailed description of these charts will not be given since readers can draw their own conclusions depending upon the intended use of the charts. However, some remarks will be made concerning spatial characteristics and magnitudes of the Q_t anomaly patterns.

The anomaly patterns of total heat exchange Q_t vary widely over the chart for a particular month and from month-to-month during the 11-yr period. Magnitudes of the Q_t anomalies range from less than 1% of the monthly average values to over 200%, with the largest values occurring in summer months. In addition, there appears to be very little month-to-month persistence in the Q_t anomaly patterns. This result is not surprising, since there is also very little persistence in the anomaly patterns of the four heat exchange terms that determine Q_t.

Since anomalies of Q_i and Q_b are usually small compared to those of Q_e and Q_s, spatial and temporal variations in Q_t anomalies are primarily due to fluctuations of evaporative and sensible heat flux. Anomaly patterns of Q_e and Q_s tend to be fairly large in geographical scope and coherence; at times, more than 50% of the eastern North Pacific is covered by an anomaly pattern of the same sign and magnitude. In addition, magnitudes of the anomalies can vary widely from month-to-month, ranging from less than 1% to over 100% of the monthly average.

Long-Term Mean or Normal Charts

In order to facilitate description of the heat exchange normals, the first two harmonics (first harmonic has a period equal to 1 yr or 12 mo) of the Fourier Series for each heat exchange term were computed for each of the 93 5° quadrangles on the chart. In addition to the two Fourier coefficients, the percentage of series variance accounted for by each of the harmonics was also computed. This type of analysis was useful in interpreting seasonal cycles of the data, since the two harmonics usually accounted for over 95% of the variance in each quadrangle; in fact, over most areas of the chart the first harmonic or yearly cycle accounted for over 90% of the variance. By deermining the phase of the harmonics, it was also possible to compare relative times of maximum and minimum values of each series.

Part 2 of the chart section shows the long-term mean monthly values (normals) of the total heat flux across the air-sea interface, $\overline{Q}_t$. Negative values of $\overline{Q}_t$, implying heat loss from the ocean surface, occur from September through March, while positive values, implying heat gain by the surface layer, occur from March through September. A regular yearly cycle is found in the $\overline{Q}_t$ series with maximum values occurring in June and minimum values in December.

Part 3 of the chart section shows the normal values of net incoming solar radiation, $\overline{Q}_i$. As expected, a regular yearly cycle is found in the $\overline{Q}_i$ series with maximum values in each quadrangle occurring in June and minimum values in December due to the motion of the earth around the sun and the tilt of the earth's axis of rotation with respect to the plane of revolution.

Part 4 of the chart section shows the effective back radiation, $\overline{Q}_b$. A regular yearly cycle is also found in the $\overline{Q}_b$ series. Maximum values occur in December and January due to the relatively low values of air vapor pressure and large values of sea-air temperature differences during these months, while minimum values occur in June and July.

Part 5 of the chart section shows the normal values of evaporative heat transfer between ocean and atmosphere, $\overline{Q}_e$. A pronounced yearly cycle is found in the $\overline{Q}_e$ series with maximum values occurring in December and minimum values in June. Negative values of $\overline{Q}_e$ occur in all months, reflecting the fact that on the average sea-air vapor pressure differences are positive throughout the year.

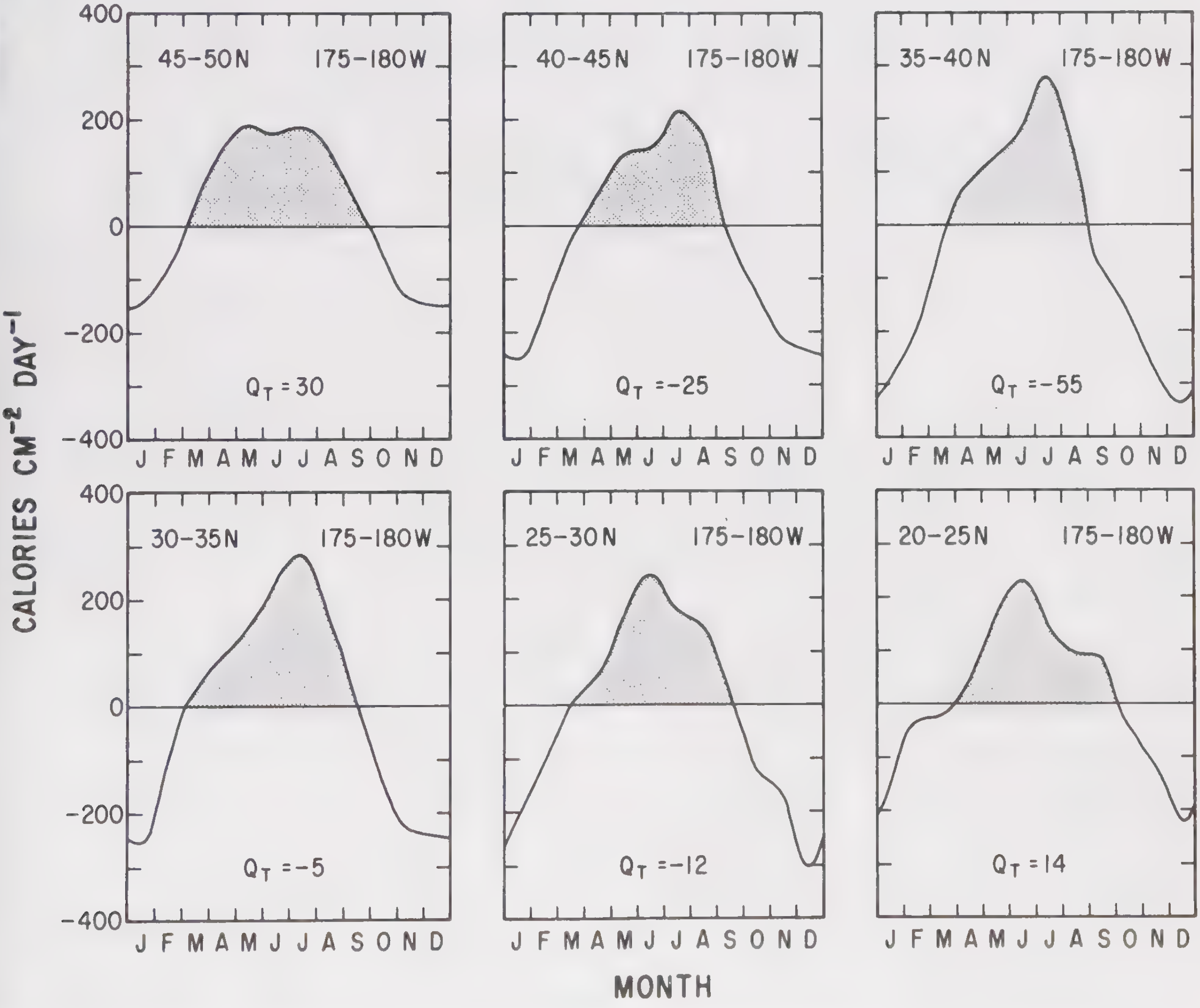

Plate 1.—Seasonal variation of average monthly total heat exchange, $\overline{Q}_t$, by 5° quadrangles from lat. 20° to 50°N in the meridional strip long. 175°W to the 180° meridian. Q_T is the average annual total heat exchange.

Part 6 of the chart section shows the normal values of sensible heat transfer between ocean and atmosphere, $\overline{Q}_S$. A regular yearly cycle is also found in the $\overline{Q}_S$ series with maximum values occurring in November and December and minimum values in May and June. Positive values of $\overline{Q}_S$ (heat gained by sea surface) occur in high latitudes from April through September, reflecting the fact that air temperatures in this region of the eastern North Pacific are warmer than sea temperatures during these months.

The yearly cycles in $\overline{Q}_e$ and $\overline{Q}_S$ reflect the fact that sea-air temperature and vapor pressure differences and observed wind speeds also have regular yearly cycles with maxima and minima that occur at the same times as those of the heat flux terms.

Seasonal Variation of the Normal Total Heat Exchange

The seasonal variation of the 1961-71 normal monthly total heat exchange, $\overline{Q}_t$, was plotted for each 5° quadrangle and the annual average computed from the equation, $Q_T = \frac{1}{12} \sum_{i=1}^{12} \overline{Q}_{ti}$,

where *i* represents the month. Except in the near coastal region of North America, the character of the normal seasonal variation changes less with latitude than with longitude. Therefore, for the oceanic region lat. 20° to 50°N and long. 130°W to 180°, the seasonal curves and the average annual values are shown here for only three selected meridional strips. Plate 1 shows the seasonal variation for each 5° quadrangle in the longitudinal strip between long. 175°W and 180° at the western boundary of the area. Similarly, Plate 2 represents the area between long. 150° and 155°W northward from Hawaii toward Kodiak, and Plate 3 represents the area between long. 130° and

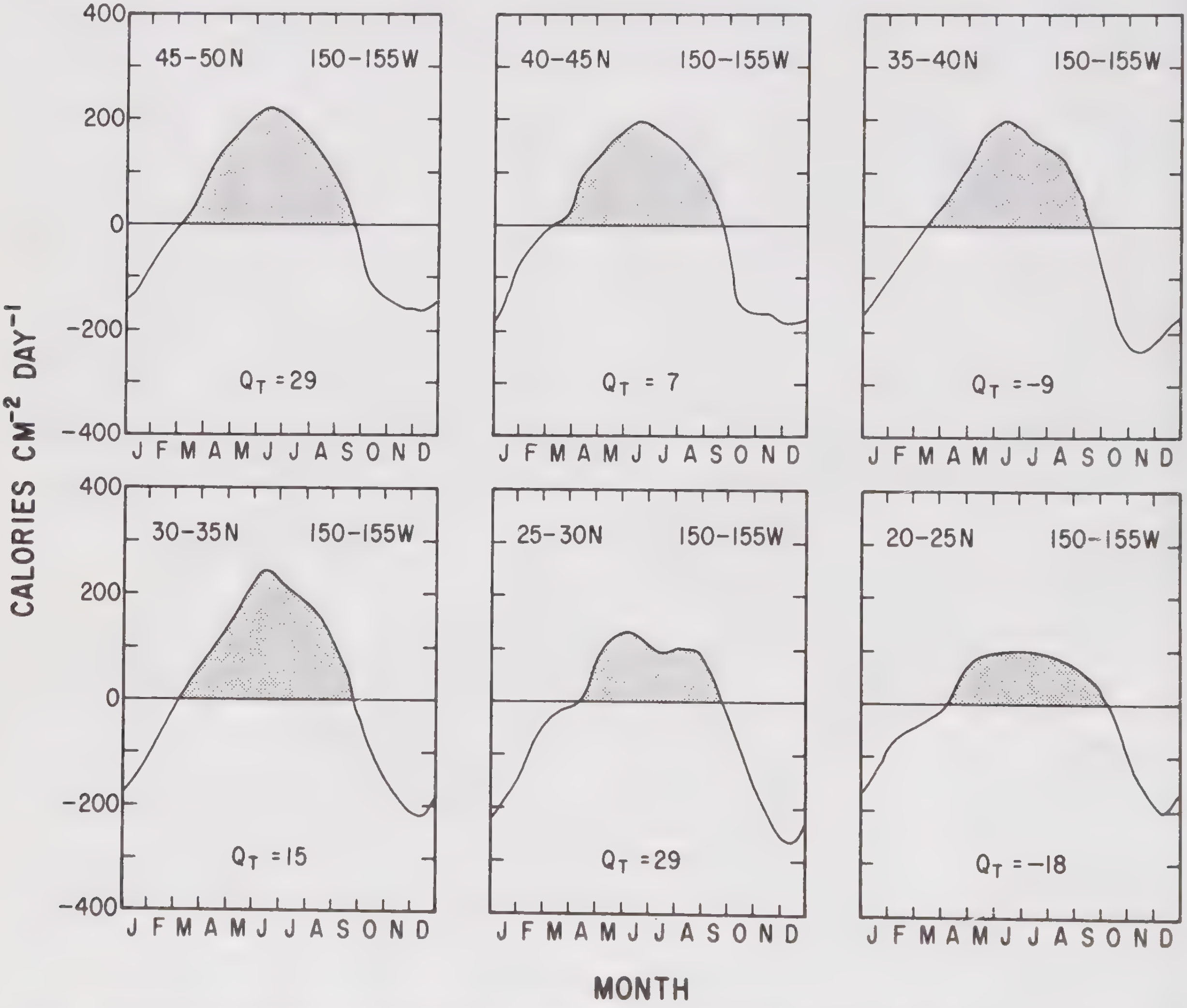

Plate 2.—Seasonal variation of average monthly total heat exchange, $\overline{Q}_t$, by 5° quadrangles from lat. 20° to 50°N in the meridional strip long. 150° to 155°W. Q_T is the average annual total heat exchange.

5°W just westward of the strong influence of the ontinental boundary. Plates 4 and 5 show the seanal variation in 5° quadrangles in coastal regions om the northern Gulf of Alaska to Washington and om Oregon to Baja California, respectively.

The general character of the seasonal variations can e described in terms of the average annual net heat xchange, the range of the variations and the months which the maximum and minimum values occur. In ne open ocean, lat. 20° to 50°N and long. 130°W to 80°, the distribution of average annual net heat exhange, Q_T, is highly zonal with the largest (positive) alues occurring in the lat. 45° to 50°N band. To the est of long. 155°W a secondary maximum appears in ne lat. 30° to 35°N band. The maximum seasonal *ange,* nearly 600 cal/cm²/day, occurs in the lat. 35° to 0°N, long. 175°W to 180° quadrangle. The lowest seaonal ranges (205 to 230 cal/cm²/day) occur in the lat. 20° to 25°N band between long. 125° and 145°W. The maximum monthly heat exchange (greatest rate of heat gain by the ocean) occurs in June in all but a few quadrangles where peak gains are in May or July and with the exception of the area from Baja California west to long. 140°W in which August maximums dominate. Minimum values (greatest rate of heat loss from the ocean) generally occur in December except for a few quadrangles with November or January minimums.

In the coastal regions the ranges of the average seasonal variation are consistently large, from about 430 to 525 cal/cm²/day from the Gulf of Alaska to the central California coast. In the northern portion of the section the annual average Q_T is negative. In the absence of declining average annual sea temperatures, a negative annual Q_T implies that heat is transported into the region by currents. Similarly, in the southern region, in the absence of increasing average annual sea

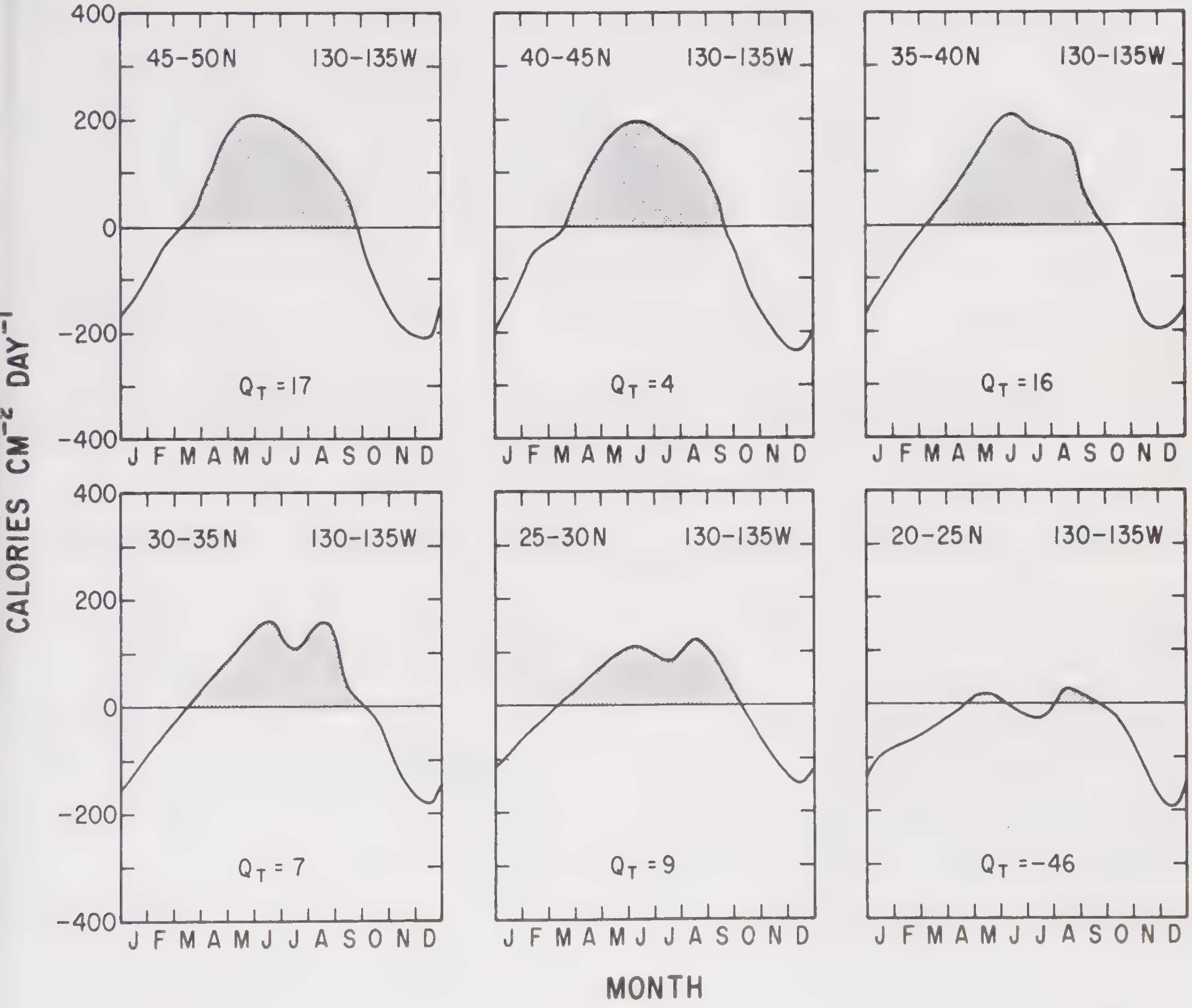

Plate 3.—Seasonal variation of average monthly total heat exchange, $\overline{Q}_t$, by 5° quadrangles from lat. 20° to 50°N in the meridional strip long. 130° to 135°W. Q_T is the average annual total heat exchange.

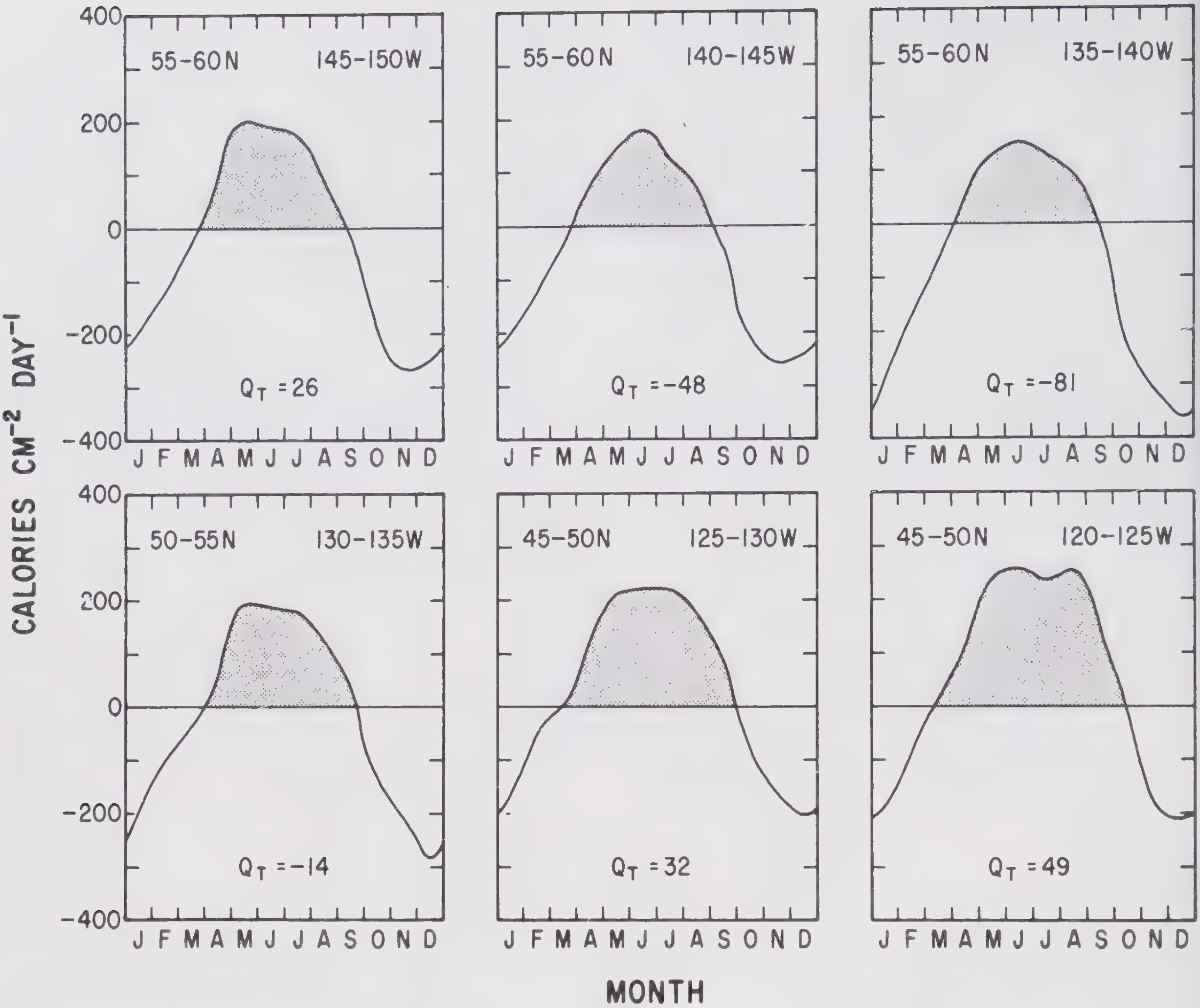

Plate 4.—Seasonal variation of average monthly total heat exchange, $\overline{Q_t}$, in coastal regions from northern Gulf of Alaska to Washington. Q_T is the average annual total heat exchange.

temperatures, a positive annual Q_T implies that heat is extracted from the region by currents.

EVALUATION OF THE CHARTS

The validity of these charts as quantitative representations of heat flux across the sea surface is subject to the quality and geographical coverage of the source data, the accuracy of the empirically derived formulas used for computation and the method of processing. Seckel (1970) has made a thorough analysis of each of these factors in producing a 2-yr series of monthly heat exchange tabulations by 5° quadrangles for the North Pacific trade wind zone. Seckel's tabulations provide an excellent set of heat flux values for comparison with those presented in this report.

Both were based on marine synoptic weather observations as the principal data source. However, for our report we utilized observations radioed ashore, while Seckel's data were derived from written logs archived by the National Weather Records Center.[2] Sets of data acquired by these two methods for particular areas and time periods will be similar but not identical due to card-punching and transmission errors and to the fact that not all data entered in weather logs are transmitted by radio, and not all observations reported by radio reach the archives.

Seckel's method of averaging the observations for each 5° quadrangle and month gave equal weight by 1° quadrangle and by day. These weighted averages of the variables needed for heat exchange computations were plotted on charts at the mean locations of the observa-

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[2] Now the National Climatic Center, National Oceanic and Atmospheric Administration.

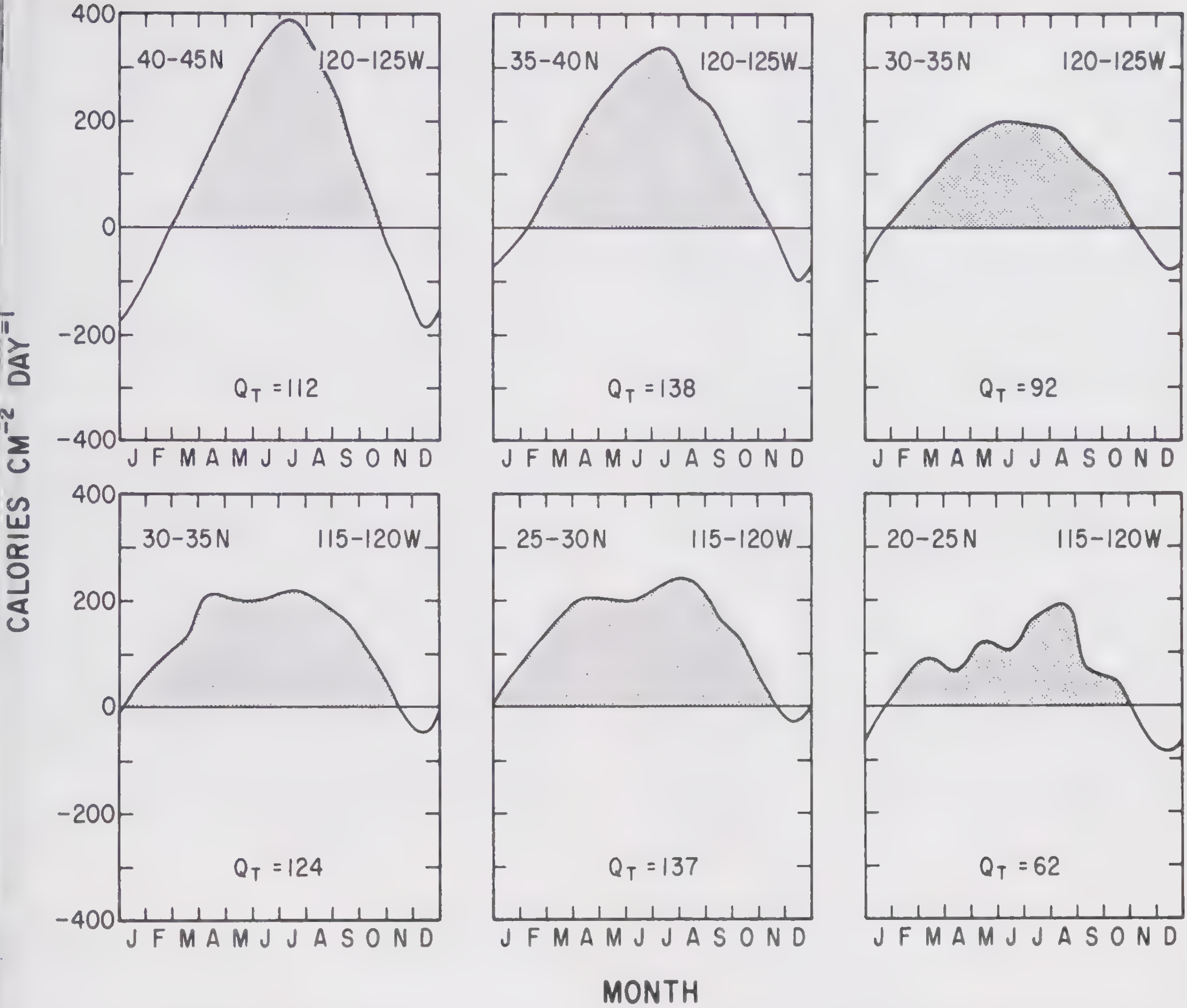

Plate 5.—Seasonal variation of average monthly total heat exchange, $\overline{Q}_t$, in coastal regions from Oregon to Baja California. Q_T is the average annual total heat exchange.

ions. The charts were then contoured and used to obtain values of each variable at the centers of the 5° quadrangles by interpolation.

In the method of Johnson et al. (1965), which was used in the preparation of this report, unweighted averages of the meteorological variables for each 5° quadrangle and month were used to compute the heat exchange components. The refinements employed in Seckel's method improve the accuracy of his results because of the fact that obervations are concentrated along shipping routes and generally are not distributed evenly in either time or space.

The empirical equations used by Seckel to compute the components of heat exchange differ in some respects from those used to obtain the results presented in this report. The greatest difference occurs in the equations for heat loss through evaporation. Seckel used a variable drag coefficient which is formulated as a function of wind speed. His equation would give approximately the same values of evaporation as that of Johnson et al. (1965) at a wind speed of about 7 m/sec.

The equation for incoming radiation employing Berliand's table, used by Johnson et al. (1965), gives higher values of heat flux than the corresponding equation used by Seckel for equivalent conditions. Computed values of sensible heat conduction, on the other hand, would be 25% greater in magnitude using Seckel's equation due to a difference in constants. The equations used for effective back radiation are the same.

In consequence, discrepancies between values of total heat exchange given in this report and those published by Seckel may arise from differences in the empirical equations, from differences in processing techniques and from differences in the observational data actually used for computation due to different methods of acquisition.

No attempt will be made to make a critical evaluation of these factors, however, a simple comparison of independently computed net heat flux values may be helpful in the utilization of the charts in this report.

The region studied by Seckel overlapped that represented by our charts from long. 130° to 170°W, between lat. 20° and 35°N. This comprises 24 5° quadrangles; consequently, 24 pairs of computed net heat flux values were available for comparison for each of the 24 mo of Seckel's series, which ran from July 1963 through June 1965.

The mean difference and the root mean square (RMS) difference of net heat flux for each 5° quadrangle are given in Table 1.

Positive differences are predominant and indicate that Seckel's values of net heat flux are larger. The RMS differences range from 40 to 106 cal/cm²/day and are generally smallest in areas having the most observations. The RMS difference for the entire sample is 72 cal/cm²/day.

Correlation coefficients were also computed for each 5° quadrangle from paired values of monthly heat flux over the 2-yr period. The results ranged from 0.93 to 0.98 for areas lat. 30° to 35°N, 0.88 to 0.95 for areas lat. 25° to 30°N, and 0.62 to 0.91 for areas lat. 20° to 25°N. Only three quadrangles had a correlation coefficient smaller than 0.86 which reflects the fact that the seasonal cycle of net heat flux, as represented by both sets of computations, is several times larger than the RMS differences. Furthermore, the apparen improvement of correlation with latitude reflects an increase in the seasonal range of heat flux northward from lat. 20° to 35°N. The areas for which the correlations were lowest were also the areas with the least observations.

Averaging over larger areas reduces the effect of random variations which adversely affect the correlation by 5° quadrangles between the two sets of values. Figure 2 shows Seckel's monthly total heat flux averaged for the entire region from long. 130° to 170°W and from lat. 20° to 35°N plotted against corresponding averages from our data. The correlation coefficient for the 24 pairs of monthly averages is 0.99 indicating that the effect of random differences has been essentially eliminated.

Systematic differences, however, are revealed by the regression line which crosses the horizontal axis at 12 cal/cm²/day, indicating that Seckel's formulas and processing technique give higher values of the total heat flux. Also, the slope of the regression line differs from 1.0, indicating another systematic discrepancy that stems, at least in part, from Seckel's use of a drag coefficient which varies with wind speed in the equations for evaporation and sensible heat transfer. His formulation gives higher evaporative heat loss with winds stronger than about 7 m/sec (other factors being equal) than those presented in this report, and lower evaporative heat loss with winds weaker than 7 m/sec.

Wind speed frequencies tallied from tables in Seckel's report indicate that in the region and period

Table 1.--Mean difference (upper value) and RMS difference (in parenthesis) of Q_t in cal/cm^2/day for 5° quadrangles

Long. Lat.	167° W	162° W	157° W	152° W	147° W	142° W	137° W	132° W
32° N	-34	-30	-16	-14	-1	9	36	30
	(101)	(96)	(63)	(38)	(51)	(54)	(48)	(40)
27° N	2	-3	21	39	26	39	26	9
	(106)	(55)	(79)	(80)	(52)	(69)	(59)	(51)
22° N	66	16	29	-5	-9	20	8	23
	(91)	(73)	(64)	(55)	(63)	(96)	(89)	(93)

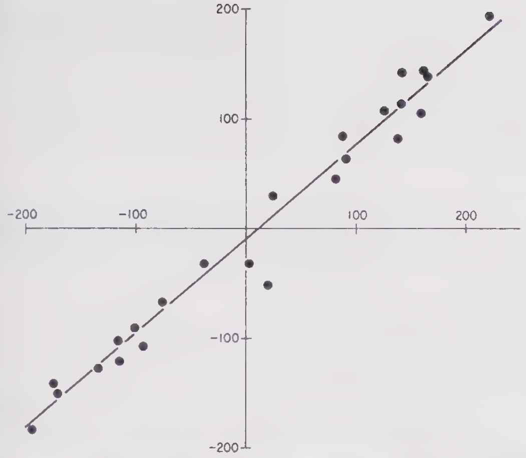

Figure 2.—Comparison of total heat transfer values (cal/cm²/day) taken from Seckel (horizontal axis) and this report (vertical axis). Each of the 24 monthly values for the period July 1963 to June 1965 was averaged over the region lat. 20° to 35°N and long. 130° to 170°W.

for which the comparison was made, wind speeds were less than 7 m/sec in about two-thirds of the cases for June through September and greater than 7 m/sec in about two-thirds of the cases for November through February. These factors combine to make Seckel's computed values of heat loss by evaporation lower than ours in the warming season and greater in the cooling season, which is reflected by his higher maximum and lower minimum values of net heat flux shown in Figure 2.

Computations of heat exchange at the sea surface have also been carried out by Wyrtki (1966) who prepared charts of heat loss by evaporation and of total heat exchange for the Pacific Ocean north of lat. 20°S. Wyrtki's charts are based on marine synoptic weather observations taken during the period 1947-60. The equations used for computation of the various components are equivalent to those described in this report, except for differences in certain empirical constants which give Wyrtki larger values of heat loss by evaporation and conduction under otherwise similar conditions. Wyrtki's method of data processing also differed from that of Johnson et al. (1965). Considering all circumstances, however, results obtained with the equations and procedures of Johnson et al. (1965) for a given set of data would probably agree as well or better with corresponding results from Wyrtki's method than with Seckel's.

Since Wyrtki's charts represent a time period antecedent to the 11 yr covered by our charts, they afford an opportunity to verify climatological patterns of net heat flux and, with caution, to infer changes in such patterns. We will make no attempt at interpretive comparison in this respect, other than to point out a few of the main characteristics in the mean cycle of heat exchange.

The beginning of the cooling season is first evident in September in the northernmost part of the Gulf of Alaska and in an area west of long. 155°W between lat. 35° and 45°N. However, large positive heat flux values still occur at this time of year along the North American coast south of lat. 45°N. By October, the mean net flux is generally negative north of lat. 25°N, except in coastal areas out to about long. 125°W. From October through January, negative heat flux is most intense in the Gulf of Alaska and west of long. 150°W, between lat. 25° and 45°N. Heat loss is minimal between lat. 45° and 50°N west of long. 165°W, and our charts show an area of positive heat flux off southern California and Baja California in every month except December. Wyrtki's charts include all of these features and, in addition, show small areas of positive heat flux even in December. In February, positive values of heat flux appear in coastal areas south of lat. 40°N, out to long. 125°W. The largest negative flux of heat at this time occurs south of lat. 30°N, from long. 165° to 170°W according to Wyrtki's charts and somewhat north and west of that area on our charts.

March is a transition month with marked intensification of positive heat flux south of lat. 40°N from the coast out to long. 125°W, while the flux elsewhere is both positive and negative and generally weak. The principal features in the heat exchange pattern which characterize spring and summer are the areas of maximum positive heat flux along central and northern California and to the west of long. 150°W at lat. 30° to 35°N. Wyrtki also found a relative maximum along the southern stretch of Baja California which does not appear on our charts because of the cutoff east of long. 115°W. A relative minimum in the pattern occurs in the vicinity of long. 130°W at about lat. 20° to 25°N. Our charts show a negative flux in this area in every month except August and September. Wyrtki found negative values in the same area in every month except July and September.

The values of net heat flux computed by Wyrtki differ from those presented in this report by 50 cal/cm²/day or more in many areas. Such differences may reflect dissimilarities in data distribution, methods of processing or real climatological trends. The main features in the mean seasonal patterns of net heat exchange depicted by our charts appear, however, to be well substantiated by comparison with those of Wyrtki.

ACKNOWLEDGMENTS

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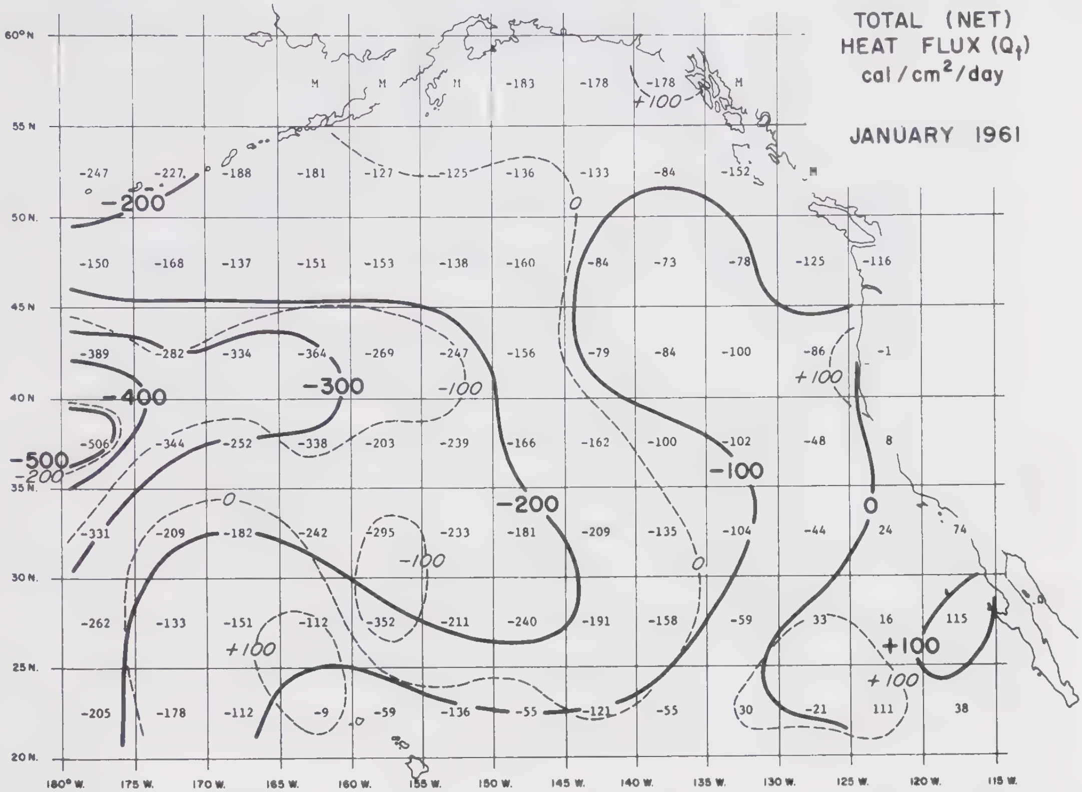
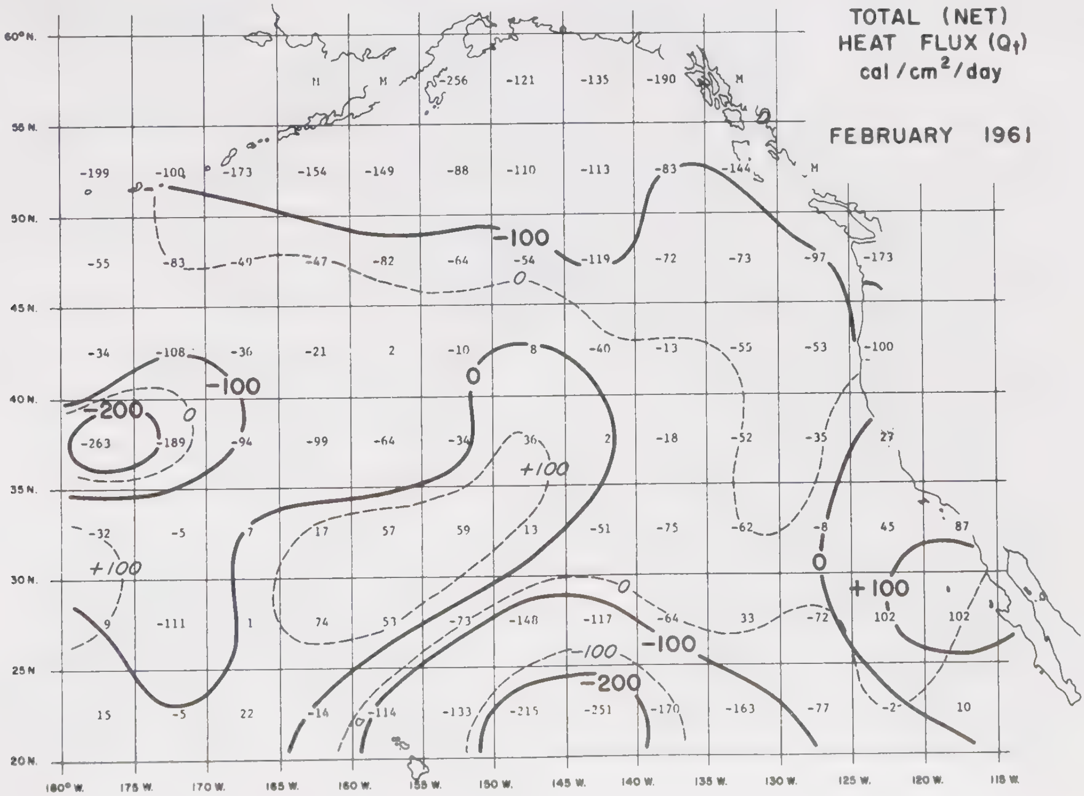
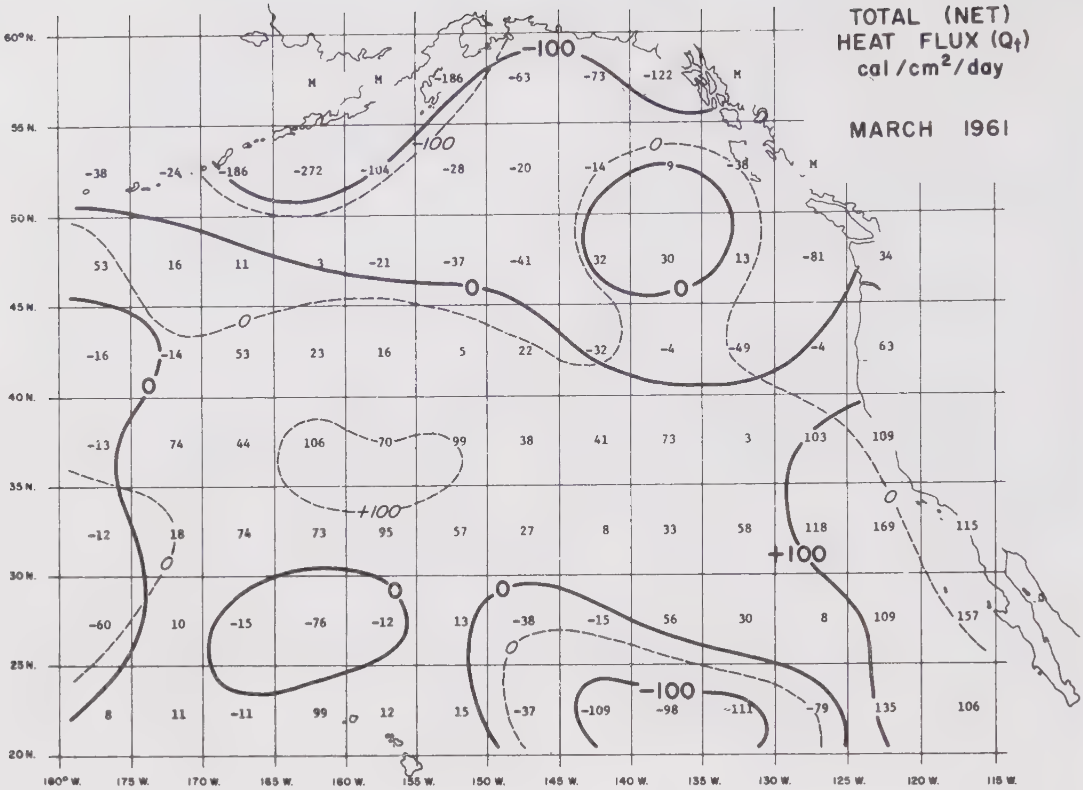
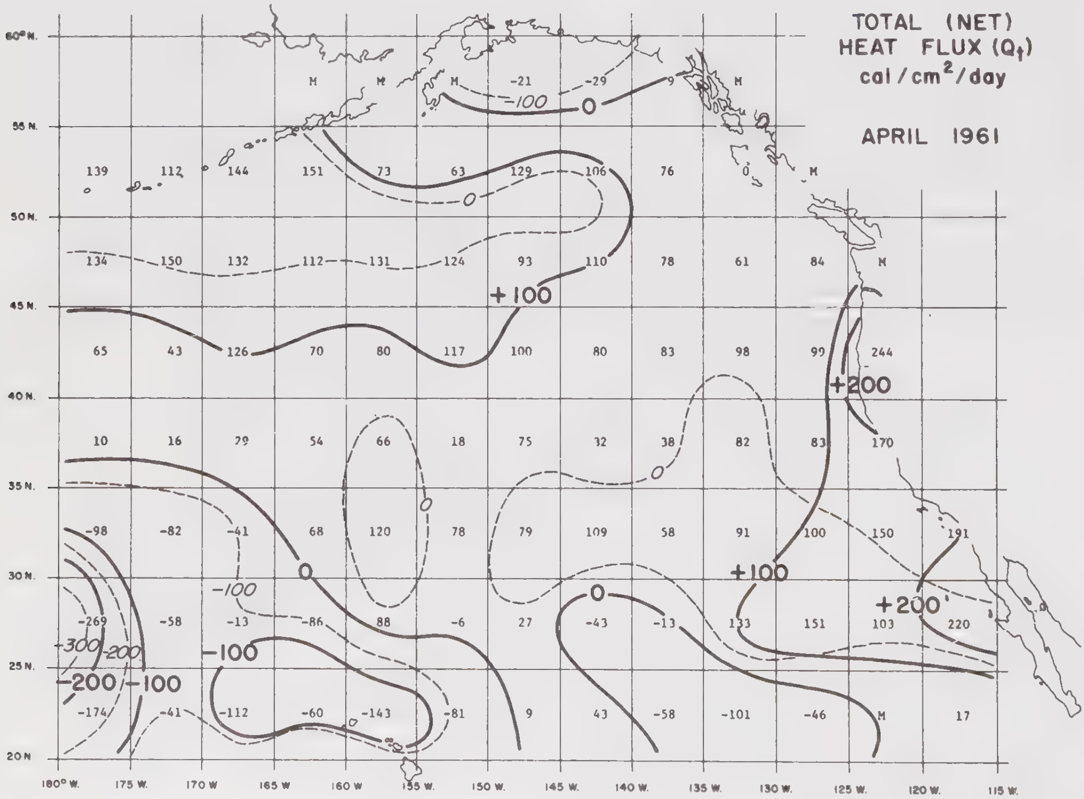
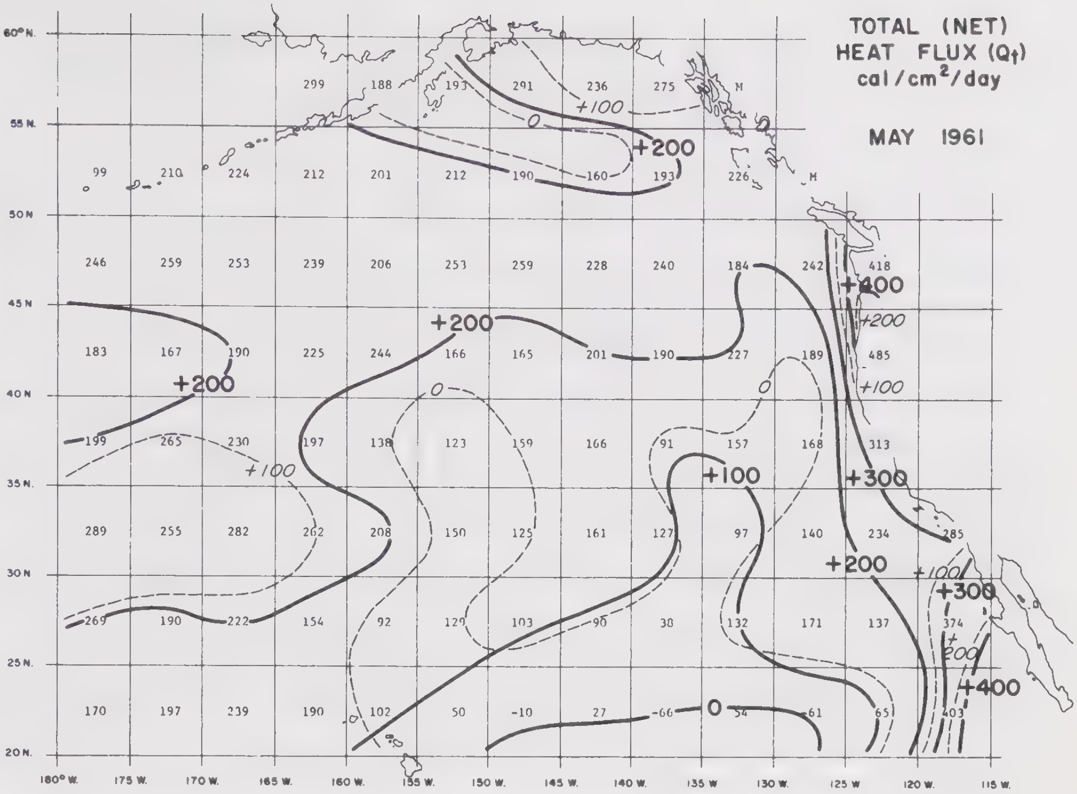
PART 1. TOTAL (NET) HEAT FLUX MONTHLY AVERAGES AND ANOMALIES, JANUARY 1961 TO DECEMBER 1971.


TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm² / day
JANUARY 1961
60° N
55 N
50 N.
45 N
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-500
-400
-300
-200
-100
0
+100


TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm² / day
FEBRUARY 1961
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-200
-100
0
+100

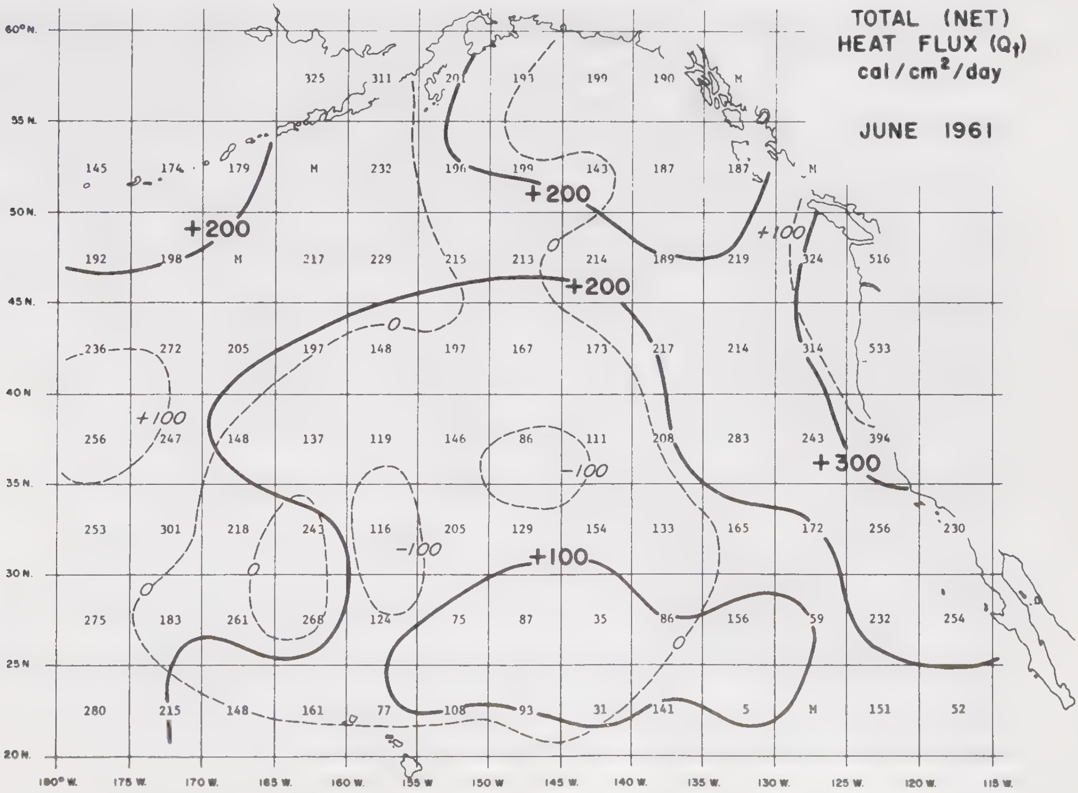

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
MARCH 1961
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M -186 -63 -73 -122 M
-38 -24 -186 -272 -104 -28 -20 -14 9 -38 M
53 16 11 3 -21 -37 -41 32 30 13 -81 34
-16 -14 53 23 16 5 22 -32 -4 -49 -4 63
-13 74 44 106 70 99 38 41 73 3 103 109
-12 18 74 73 95 57 27 8 33 58 118 169 115
-60 10 -15 -76 -12 13 -38 -15 56 30 8 109 157
8 11 -11 99 12 15 -37 -109 -98 -111 -79 135 106
-100
-100
0
+100
+100
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
APRIL 1961
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -21 -29 9 M
139 112 144 151 73 63 129 106 76 M
134 150 132 112 131 124 93 110 78 61 84 M
65 43 126 70 80 117 100 80 83 98 99 244
10 16 29 54 66 18 75 32 38 82 83 170
-98 -82 -41 68 120 78 79 109 58 91 100 150 191
-269 -58 -13 -86 88 -6 27 -43 -13 133 151 103 220
-174 -41 -112 -60 -143 -81 9 43 -58 -101 -46 M 17
-100
0
+100
-100
-300
-200
-200
-100
+100
+200
+200


TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

MAY 1961

60° N.
55 N.
50 N
45 N
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W
130 W.
125 W
120 W.
115 W.
299 188 193 291 236 275 M
99 210 224 212 201 212 190 160 193 226 M
246 259 253 239 206 253 259 228 240 184 242 418
183 167 190 225 244 166 165 201 190 227 189 485
199 265 230 197 138 123 159 166 91 157 168 313
289 255 282 262 208 150 125 161 127 97 140 234 285
269 190 222 154 92 129 103 90 38 132 171 137 374
170 197 239 190 102 50 -10 27 -66 54 61 65 403
+100
0
+200
+400
+200
+100
+200
+200
+100
+100
0
+300
+200
+100
+300
+200
+400
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

JUNE 1961

60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N.
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
325 311 201 193 199 190 M
145 174 179 M 232 196 199 143 187 187 M
192 198 M 217 229 215 213 214 189 219 324 516
236 272 205 197 148 197 167 173 217 214 314 533
256 247 148 137 119 146 86 111 208 283 243 394
253 301 218 243 116 205 129 154 133 165 172 256 230
275 183 261 268 124 75 87 35 86 156 59 232 254
280 215 148 161 77 108 93 31 141 5 M 151 52
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+200
+100
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+200
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0
-100
+100
0
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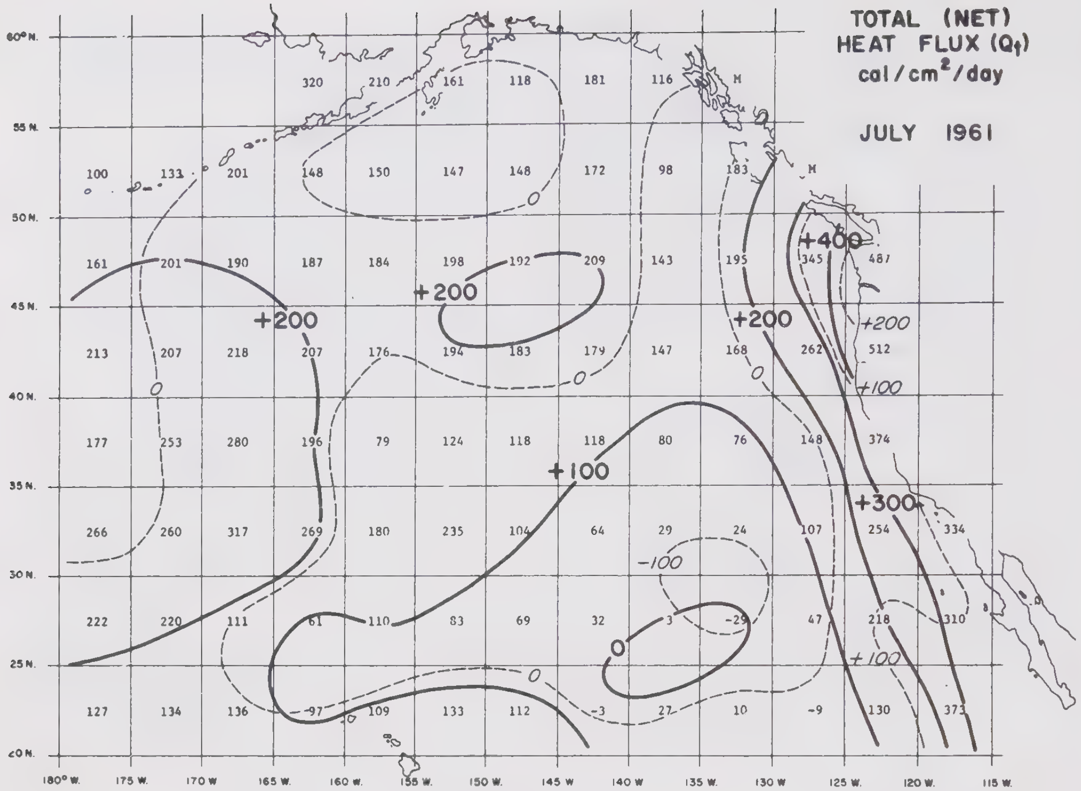
TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
JULY 1961
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W
165 W.
160 W.
155 W.
150 W.
145 W
140 W
135 W.
130 W
125 W.
120 W.
115 W.
320 210 161 118 181 116 M
100 133 201 148 150 147 148 172 98 183 M
161 201 190 187 184 198 192 209 143 195 345 487
213 207 218 207 176 194 183 179 147 168 262 512
177 253 280 196 79 124 118 118 80 76 148 374
266 260 317 269 180 235 104 64 29 24 107 254 334
222 220 111 61 110 83 69 32 3 -29 47 218 310
127 134 136 -97 109 133 112 -3 27 10 -9 130 373
+400
+200
+200
+200
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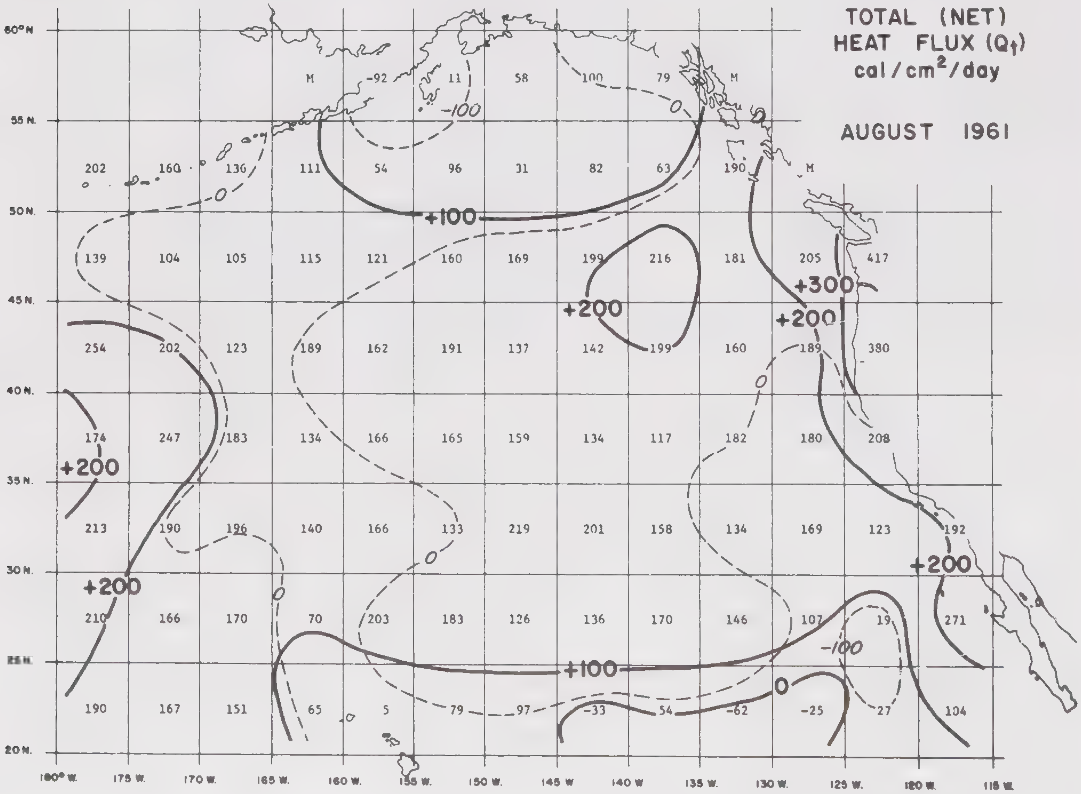
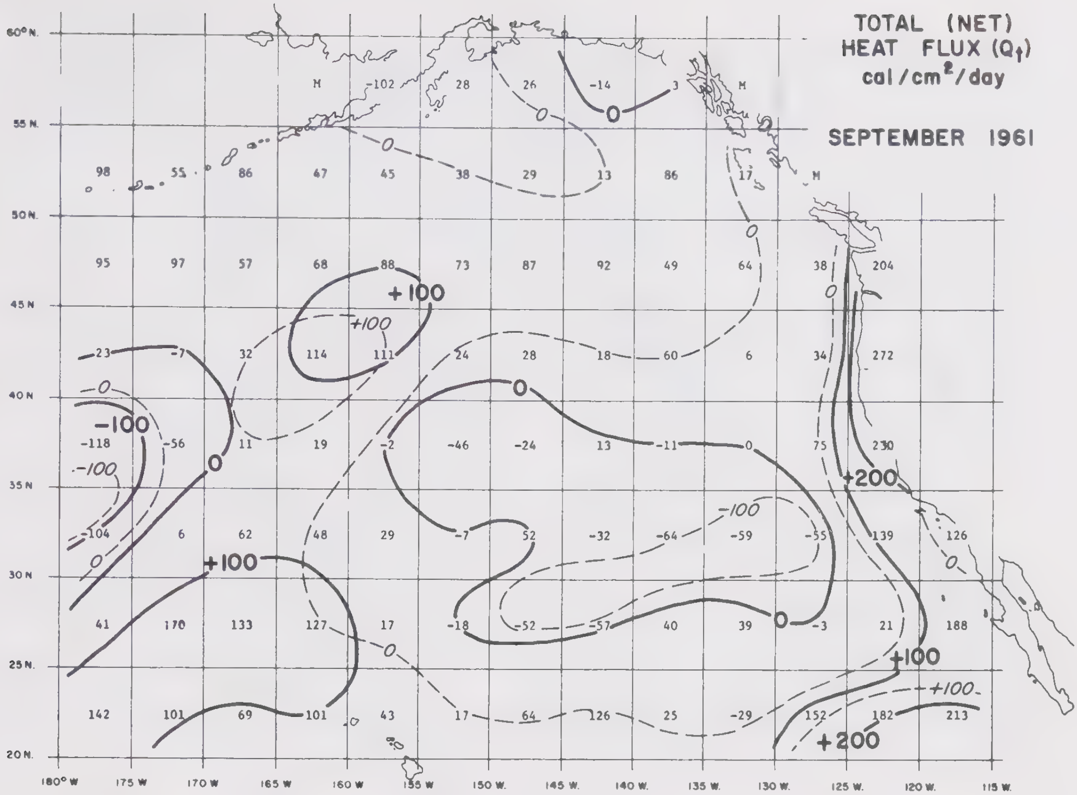
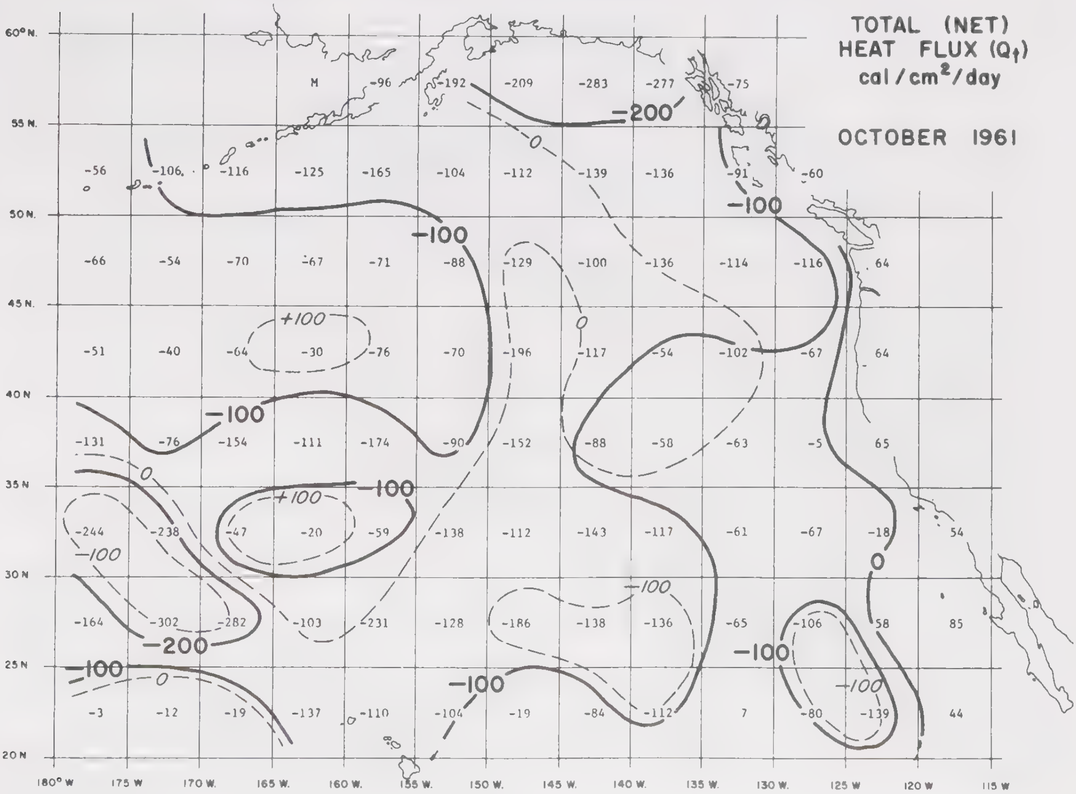

TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
AUGUST 1961
60°N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W
140 W
135 W.
130 W.
125 W.
120 W.
115 W.
M -92 11 58 100 79 M
202 160 136 111 54 96 31 82 63 190 M
139 104 105 115 121 160 169 199 216 181 205 417
254 202 123 189 162 191 137 142 199 160 189 380
174 247 183 134 166 165 159 134 117 182 180 208
213 190 196 140 166 133 219 201 158 134 169 123 192
210 166 170 70 203 183 126 136 170 146 107 19 271
190 167 151 65 5 79 97 -33 54 -62 -25 27 104
-100
+100
+100
+200
+200
+200
+200
+200
+300
-100
0
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

SEPTEMBER 1961

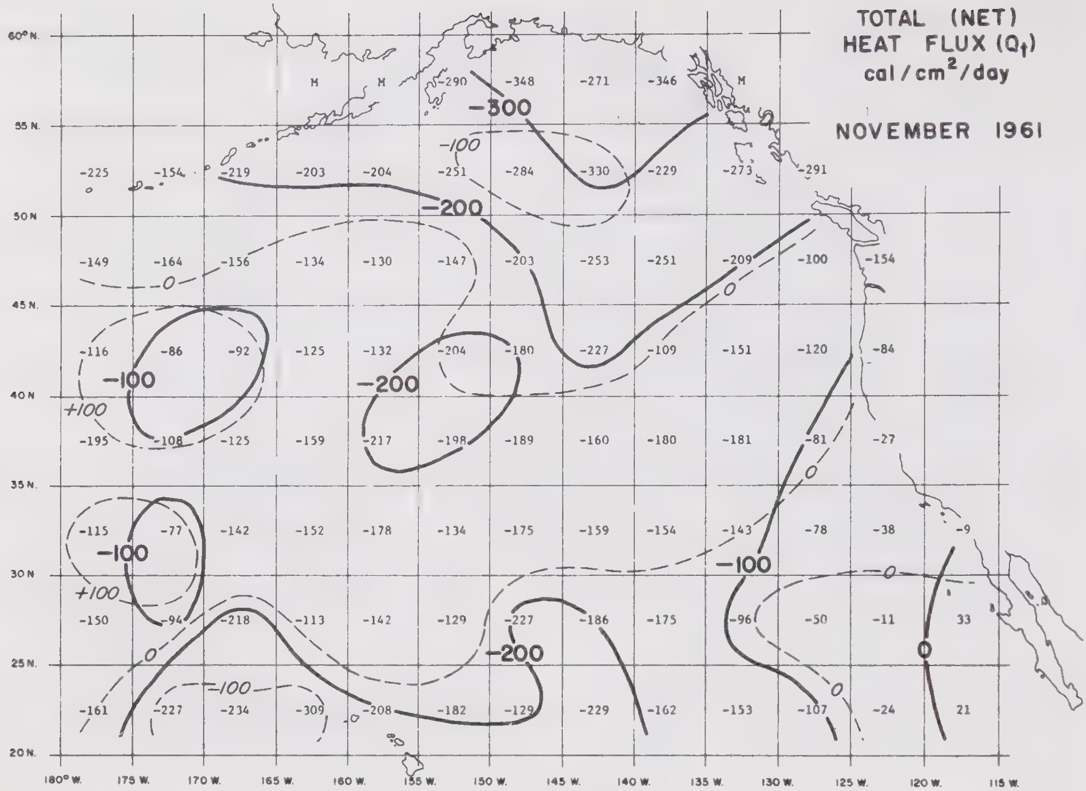
60° N.
55 N.
50 N.
45 N
40 N
35 N
30 N
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W
155 W
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
-102
28
26
-14
3
M
98
55
86
47
45
38
29
13
86
17
M
95
97
57
68
88
73
87
92
49
64
38
204
-23
-7
32
114
111
24
28
18
60
6
34
272
-118
-56
11
19
-2
-46
-24
13
-11
0
75
230
-104
6
62
48
29
-7
52
-32
-64
-59
-55
139
126
41
170
133
127
17
-18
-52
-57
40
39
-3
21
188
142
101
69
101
43
17
64
126
25
-29
152
182
213
0
+100
+100
-100
-100
+200
+100
+200

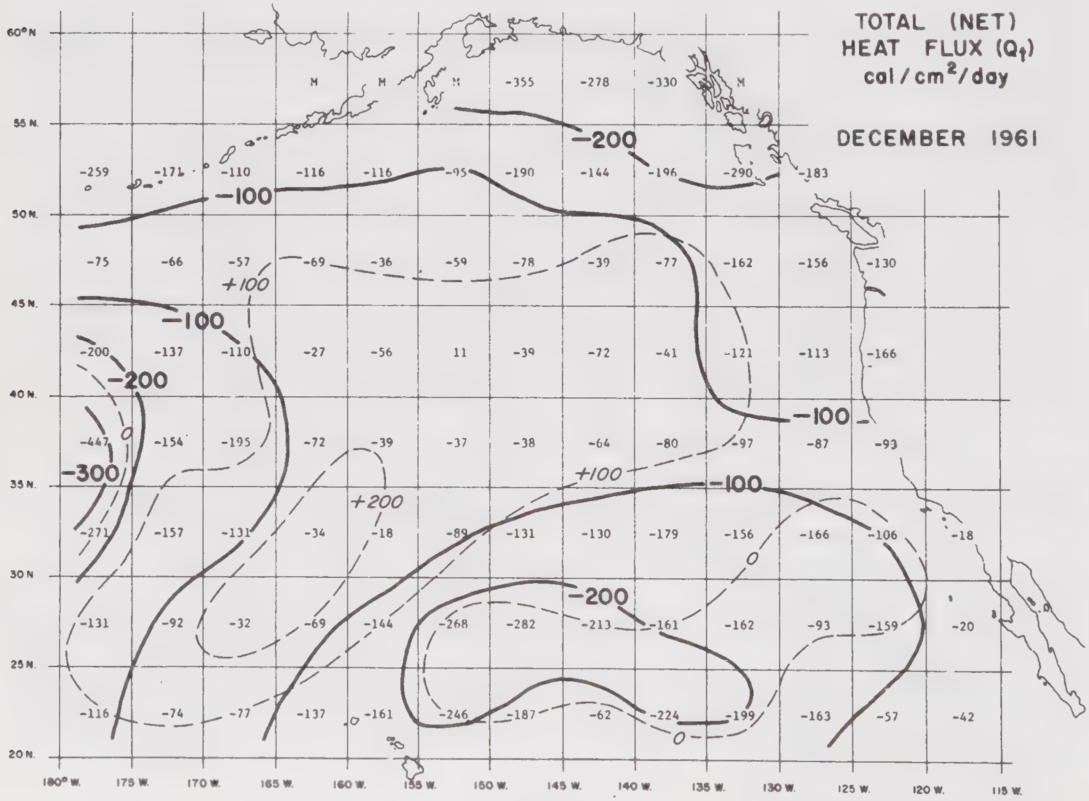


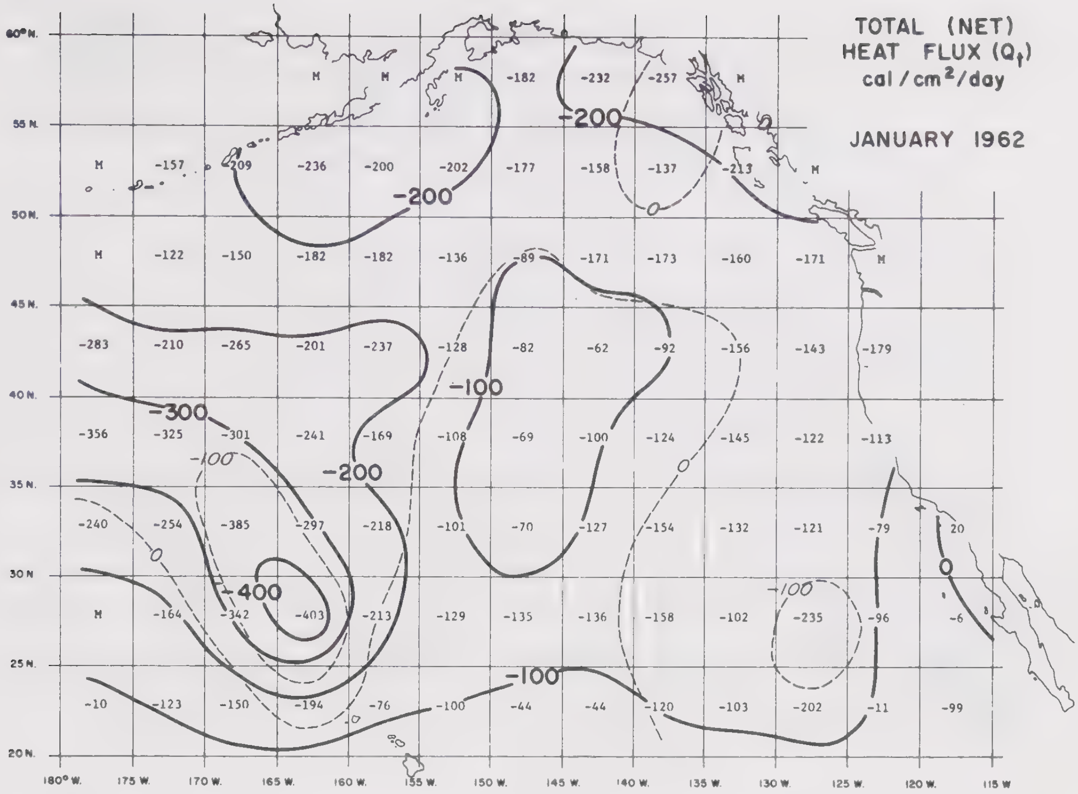
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

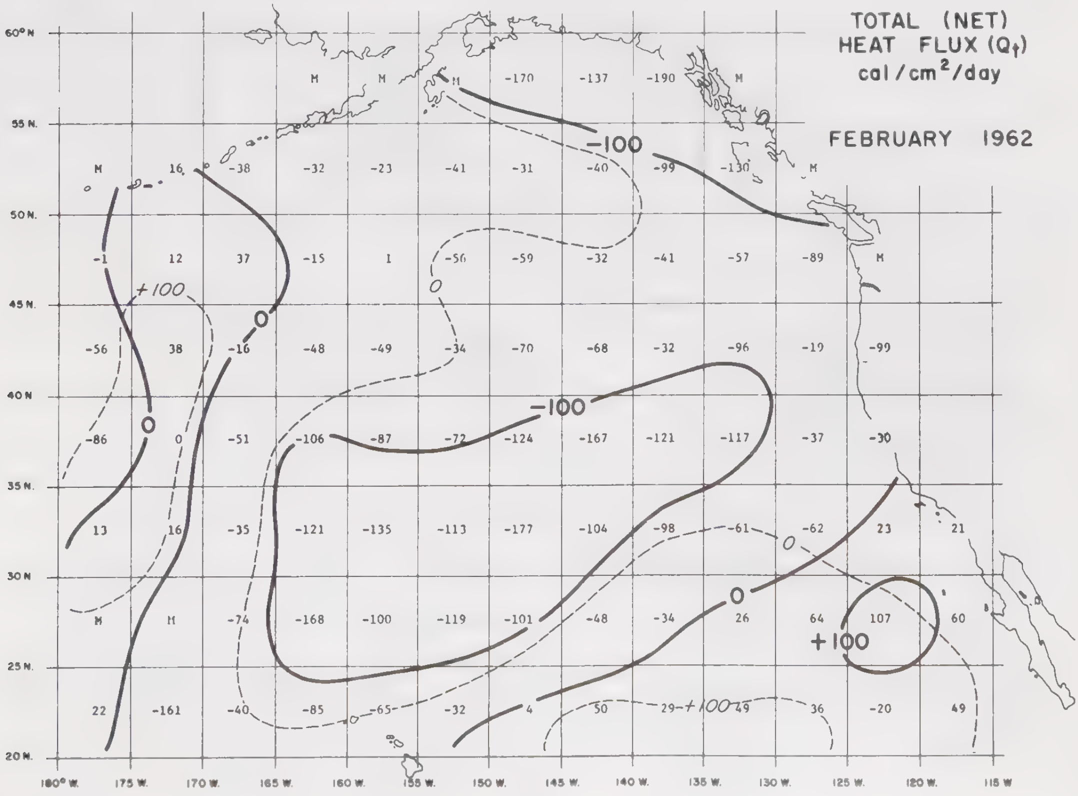
OCTOBER 1961

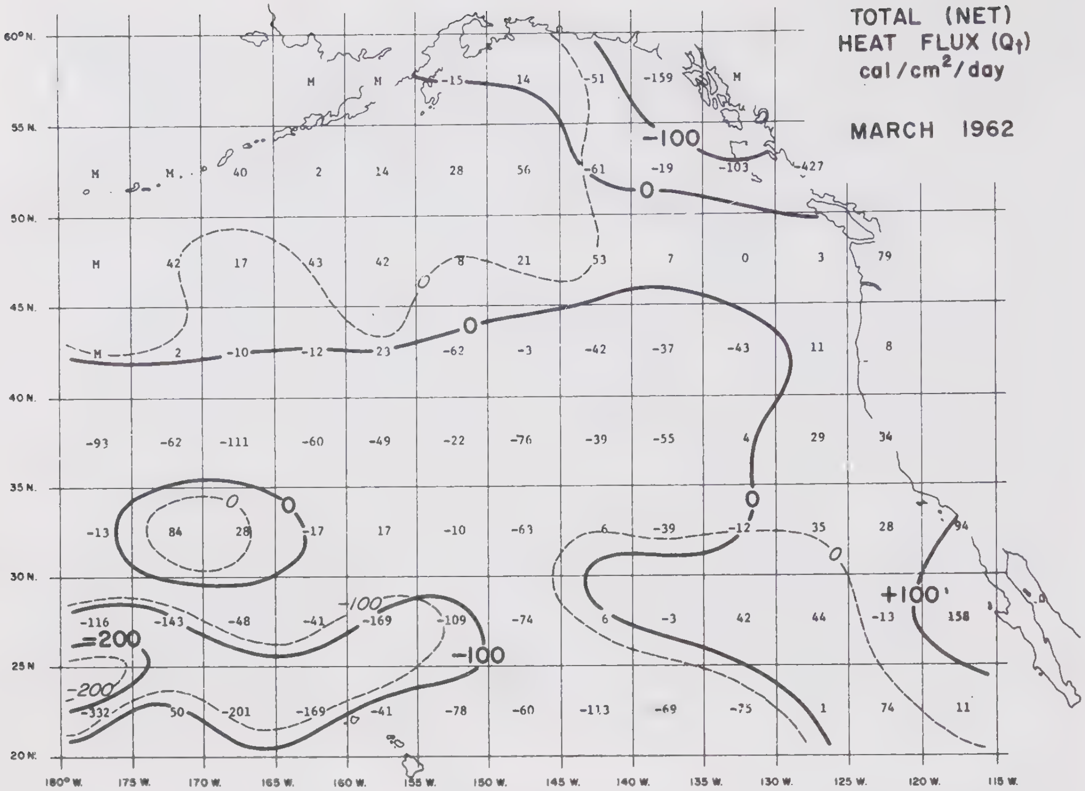
60° N.
55 N.
50 N.
45 N.
40 N
35 N
30 N
25 N
20 N
180° W
175 W
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W
120 W
115 W
M
-96
-192
-209
-283
-277
-75
-56
-106
-116
-125
-165
-104
-112
-139
-136
-91
-60
-66
-54
-70
-67
-71
-88
-129
-100
-136
-114
-116
64
-51
-40
-64
-30
-76
-70
-196
-117
-54
-102
-67
64
-131
-76
-154
-111
-174
-90
-152
-88
-58
-63
-5
65
-244
-238
-47
-20
-59
-138
-112
-143
-117
-61
-67
-18
54
-164
-302
-282
-103
-231
-128
-186
-138
-136
-65
-106
58
85
-3
-12
-19
-137
-110
-104
-19
-84
-112
7
-80
-139
44
-200
0
-100
+100
-200

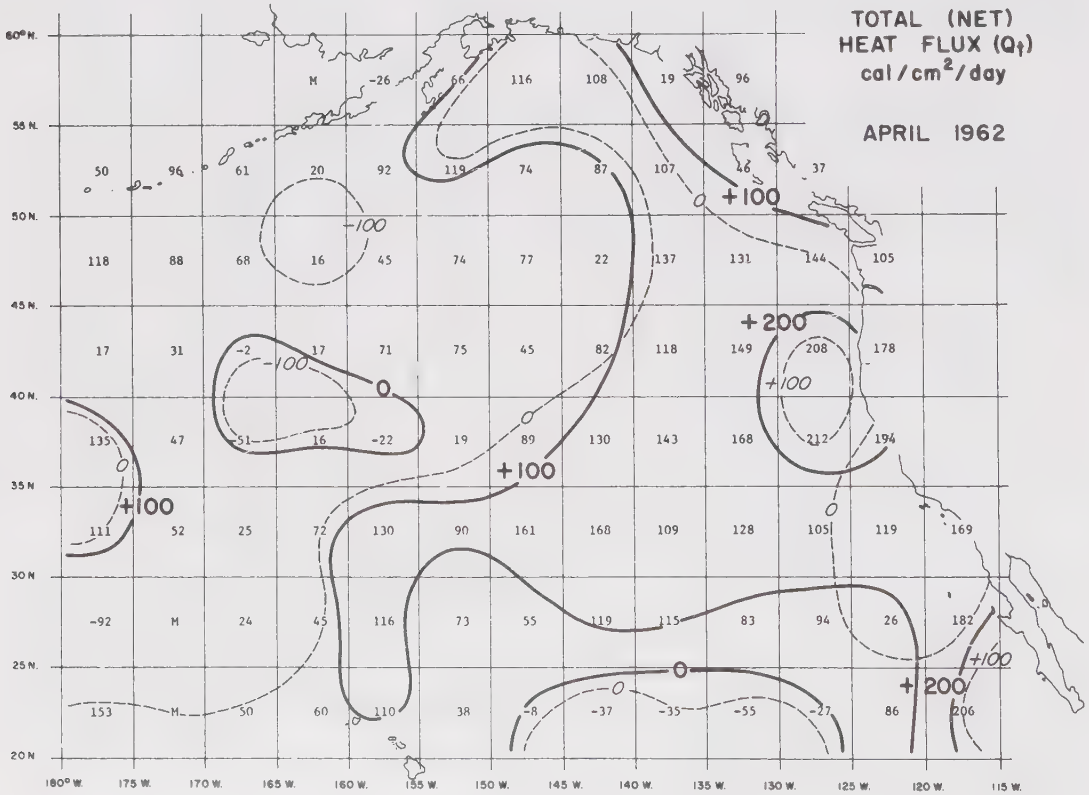

TOTAL (NET)
HEAT FLUX (Q$_t$)
cal / cm^2 / day
NOVEMBER 1961
60° N.
55 N.
50 N
45 N.
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M -290 -348 -271 -346 M
-225 -154 -219 -203 -204 -251 -284 -330 -229 -273 -291
-149 -164 -156 -134 -130 -147 -203 -253 -251 -209 -100 -154
-116 -86 -92 -125 -132 -204 -180 -227 -109 -151 -120 -84
-195 -108 -125 -159 -217 -198 -189 -160 -180 -181 -81 -27
-115 -77 -142 -152 -178 -134 -175 -159 -154 -143 -78 -38 -9
-150 -94 -218 -113 -142 -129 -227 -186 -175 -96 -50 -11 33
-161 -227 -234 -309 -208 -182 -129 -229 -162 -153 -107 -24 21
-300
-100
-200
0
-100
+100
-200
0
-100
+100
-100
0
-100
-200
0
-0
0
0

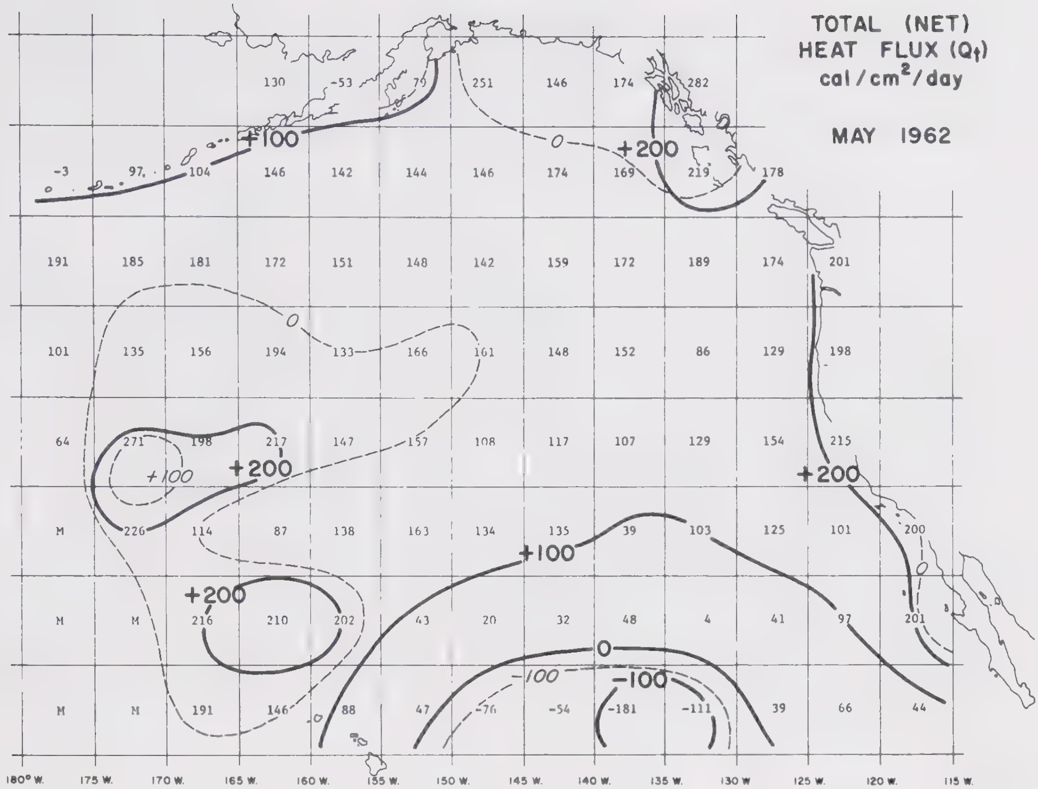

TOTAL (NET)
HEAT FLUX (Q$_t$)
cal / cm^2 / day
DECEMBER 1961
60° N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -355 -278 -330 M
-259 -171 -110 -116 -116 -95 -190 -144 -196 -290 -183
-75 -66 -57 -69 -36 -59 -78 -39 -77 -162 -156 -130
-200 -137 -110 -27 -56 11 -39 -72 -41 -121 -113 -166
-447 -154 -195 -72 -39 -37 -38 -64 -80 -97 -87 -93
-271 -157 -131 -34 -18 -89 -131 -130 -179 -156 -166 -106 -18
-131 -92 -32 -69 -144 -268 -282 -213 -161 -162 -93 -159 -20
-116 -74 -77 -137 -161 -246 -187 -62 -224 -199 -163 -57 -42
-200
-100
+100
-100
-200
0
-300
-100
+100
-100
+200
-200
0
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
JANUARY 1962
60°N. 55N. 50N. 45N. 40N. 35N. 30N. 25N. 20N.
180°W. 175W. 170W. 165W. 160W. 155W. 150W. 145W. 140W. 135W. 130W. 125W. 120W. 115W
M M M -182 -232 -257 M
M -157 -209 -236 -200 -202 -177 -158 -137 -213 M
M -122 -150 -182 -182 -136 -89 -171 -173 -160 -171 M
-283 -210 -265 -201 -237 -128 -82 -62 -92 -156 -143 -179
-356 -325 -301 -241 -169 -108 -69 -100 -124 -145 -122 -113
-240 -254 -385 -297 -218 -101 -70 -127 -154 -132 -121 -79 20
M -164 -342 -403 -213 -129 -135 -136 -158 -102 -235 -96 -6
-10 -123 -150 -194 -76 -100 -44 -44 -120 -103 -202 -11 -99
-200
-200
-300
-100
-200
-100
-400
-100
-100
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
FEBRUARY 1962
60°N 55N. 50N. 45N. 40N 35N. 30N 25N. 20N.
180°W. 175W. 170W. 165W. 160W. 155W. 150W. 145W. 140W. 135W. 130W. 125W. 120W. 115W
M M M -170 -137 -190 M
M 16 -38 -32 -23 -41 -31 -40 -99 -130 M
-1 12 37 -15 1 -56 -59 -32 -41 -57 -89 M
-56 38 -16 -48 -49 -34 -70 -68 -32 -96 -19 -99
-86 0 -51 -106 -87 -72 -124 -167 -121 -117 -37 -30
13 16 -35 -121 -135 -113 -177 -104 -98 -61 -62 23 21
M M -74 -168 -100 -119 -101 -48 -34 26 64 107 60
22 -161 -40 -85 -65 -32 4 50 29 49 36 -20 49
-100
+100
0
0
-100
0
+100
+100


TOTAL (NET)
HEAT FLUX (Q$_t$)
cal/cm^2/day
MARCH 1962
60°N.
55N.
50N.
45N.
40N.
35N.
30N.
25N
20N
180°W.
175W.
170W.
165W.
160W.
155W.
150W.
145W.
140W.
135W.
130W.
125W.
120W.
115W.
M
M
-15
14
-51
-159
M
-100
M
M
40
2
14
28
56
-61
-19
-103
-427
0
M
42
17
43
42
8
21
53
7
0
3
79
0
0
M
2
-10
-12
23
-62
-3
-42
-37
-43
11
8
-93
-62
-111
-60
-49
-22
-76
-39
-55
4
29
34
0
0
0
-13
84
28
-17
17
-10
-63
6
-39
-12
35
28
94
0
+100
-100
-116
-143
-48
-41
-169
-109
-74
6
-3
42
44
-13
158
-200
-100
-200
-332
50
-201
-169
-41
-78
-60
-113
-69
-75
1
74
11

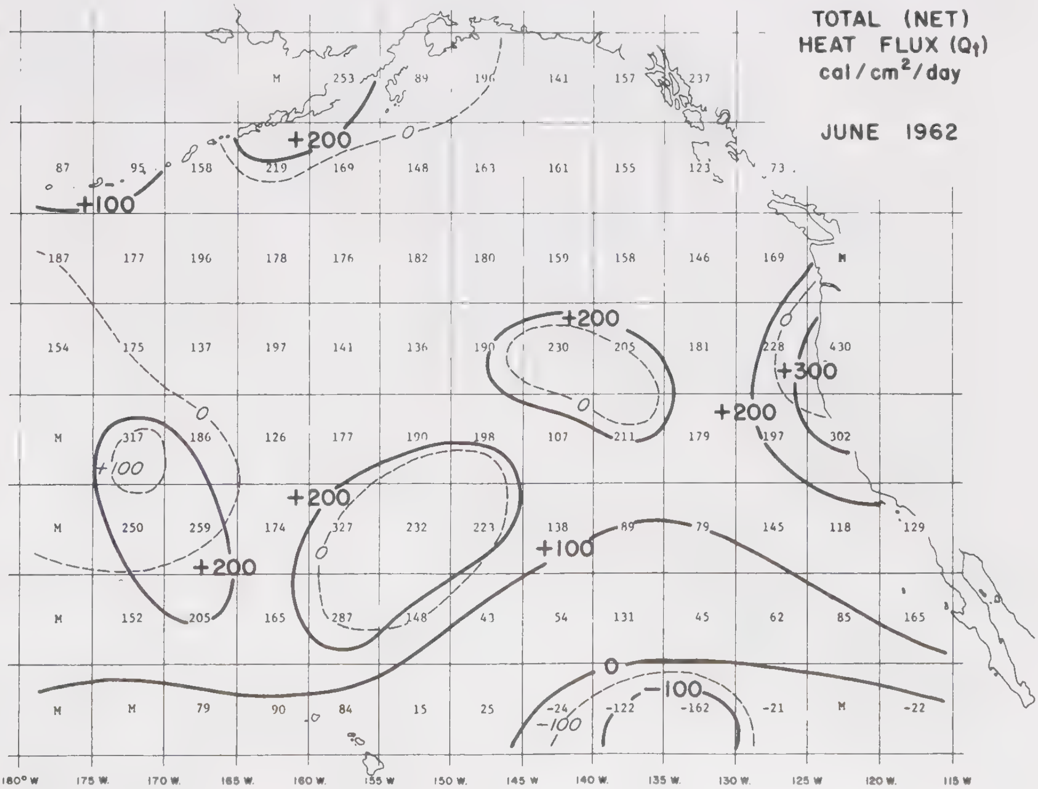

TOTAL (NET)
HEAT FLUX (Q$_t$)
cal/cm^2/day
APRIL 1962
60°N.
55N.
50N.
45N.
40N.
35N
30N
25N.
20N
180°W.
175W.
170W.
165W.
160W.
155W.
150W.
145W.
140W.
135W.
130W.
125W.
120W.
115W.
M
-26
66
116
108
19
96
50
96
61
20
92
119
74
87
107
46
37
0
+100
-100
118
88
68
16
45
74
77
22
137
131
144
105
+200
17
31
-2
-100
17
71
75
45
82
118
149
208
178
0
+100
0
135
47
-51
16
-22
19
89
130
143
168
212
194
+100
0
+100
0
111
52
25
72
130
90
161
168
109
128
105
119
169
-92
M
24
45
116
73
55
119
115
83
94
26
182
0
0
+100
+200
153
M
50
60
110
38
-8
-37
-35
-55
-27
86
206



TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day

MAY 1962

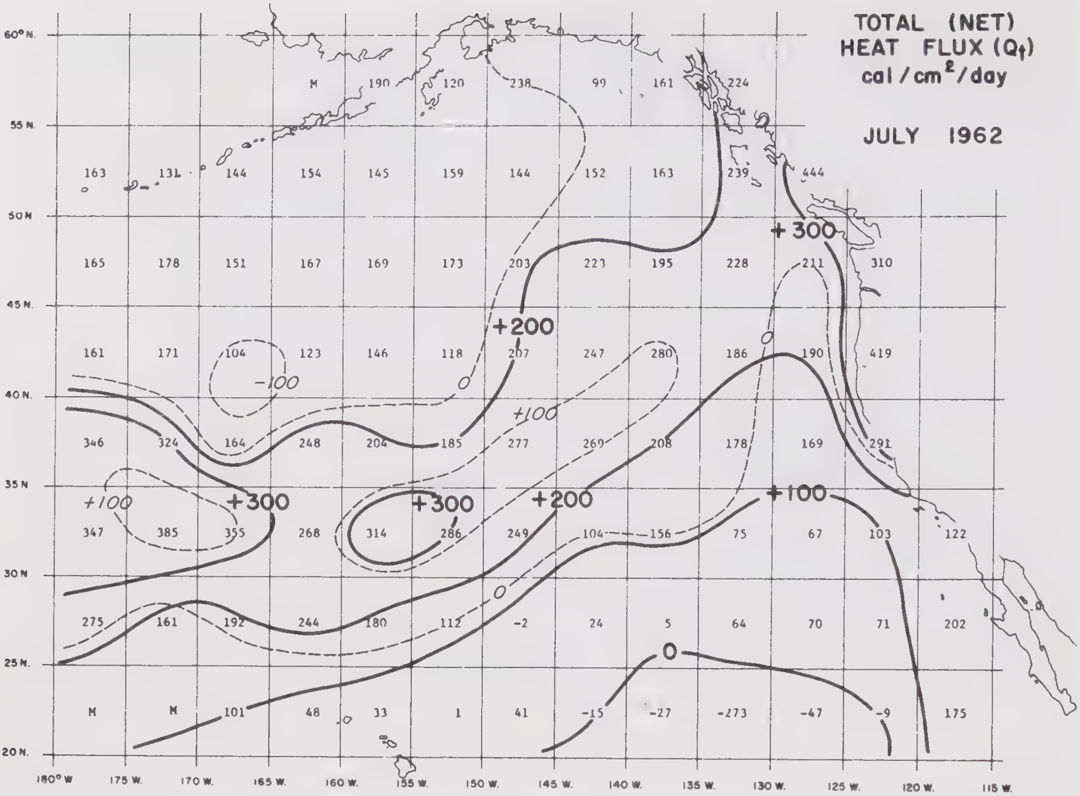
60°N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
130 -53 79 251 146 174 282
+100
0
+200
-3 97 104 146 142 144 146 174 169 219 178
191 185 181 172 151 148 142 159 172 189 174 201
0
101 135 156 194 133 166 161 148 152 86 129 198
64 271 198 217 147 157 108 117 107 129 154 215
+100
+200
+200
M 226 114 87 138 163 134 135 39 103 125 101 200
+100
0
+200
M M 216 210 202 43 20 32 48 4 41 97 201
0
-100
-100
M M 191 146 0 88 47 -76 -54 -181 -111 39 66 44



TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day

JUNE 1962

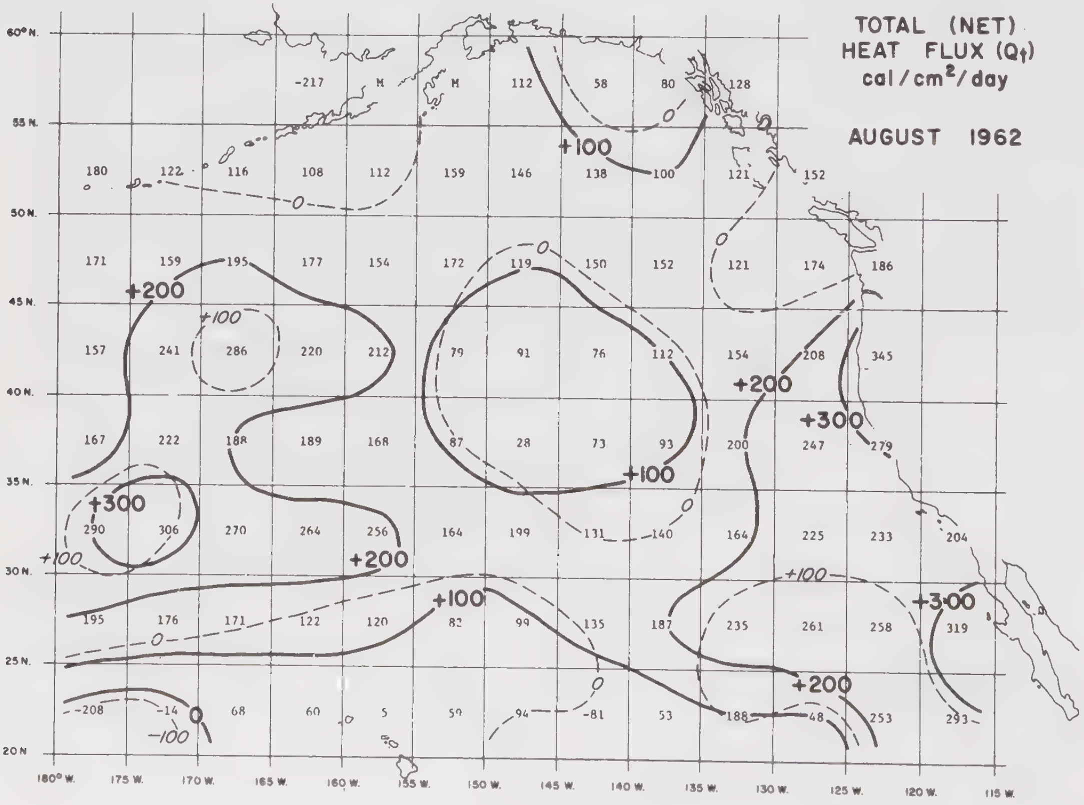
60°N
55 N.
50 N.
45 N
40 N
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W.
145 W
140 W.
135 W.
130 W.
125 W
120 W.
115 W
M 253 89 196 141 157 237
+200
0
87 95 158 219 169 148 163 161 155 123 73
+100
187 177 196 178 176 182 180 159 158 146 169 M
+200
0
154 175 137 197 141 136 190 230 205 181 228 430
+300
0
0
+200
M 317 186 126 177 190 198 107 211 179 197 302
+100
+200
M 250 259 174 327 232 223 138 89 79 145 118 129
0
+100
+200
M 152 205 165 287 148 43 54 131 45 62 85 165
0
-100
M M 79 90 0 84 15 25 -24 -122 -162 -21 M -22
-100



TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day

JULY 1962

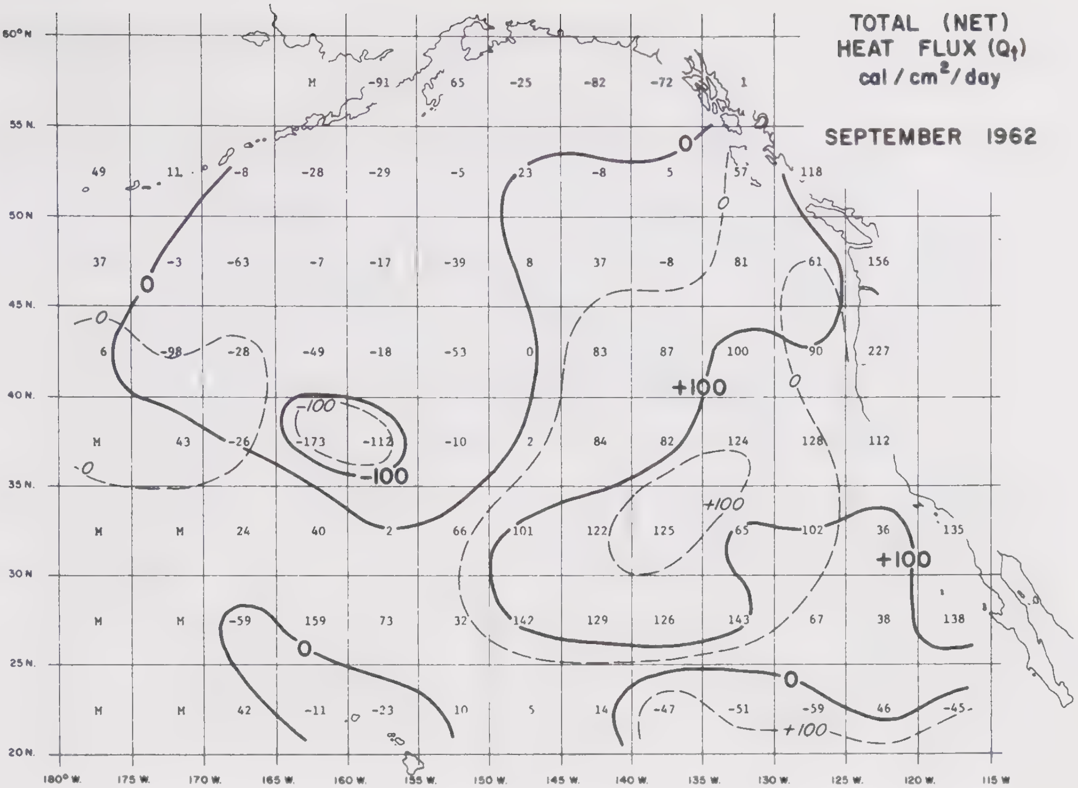
60° N.
55 N.
50 N
45 N.
40 N.
35 N
30 N
25 N.
20 N.
180° W
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M 190 120 238 99 161 224
163 131 144 154 145 159 144 152 163 239 444
165 178 151 167 169 173 203 223 195 228 211 310
161 171 104 123 146 118 207 247 280 186 190 419
346 324 164 248 204 185 277 269 208 178 169 291
347 385 355 268 314 286 249 104 156 75 67 103 122
275 161 192 244 180 112 -2 24 5 64 70 71 202
M M 101 48 33 1 41 -15 -27 -273 -47 -9 175
+300
+300
+300
+200
+200
+100
+100
+100
0
0
0
0
-100

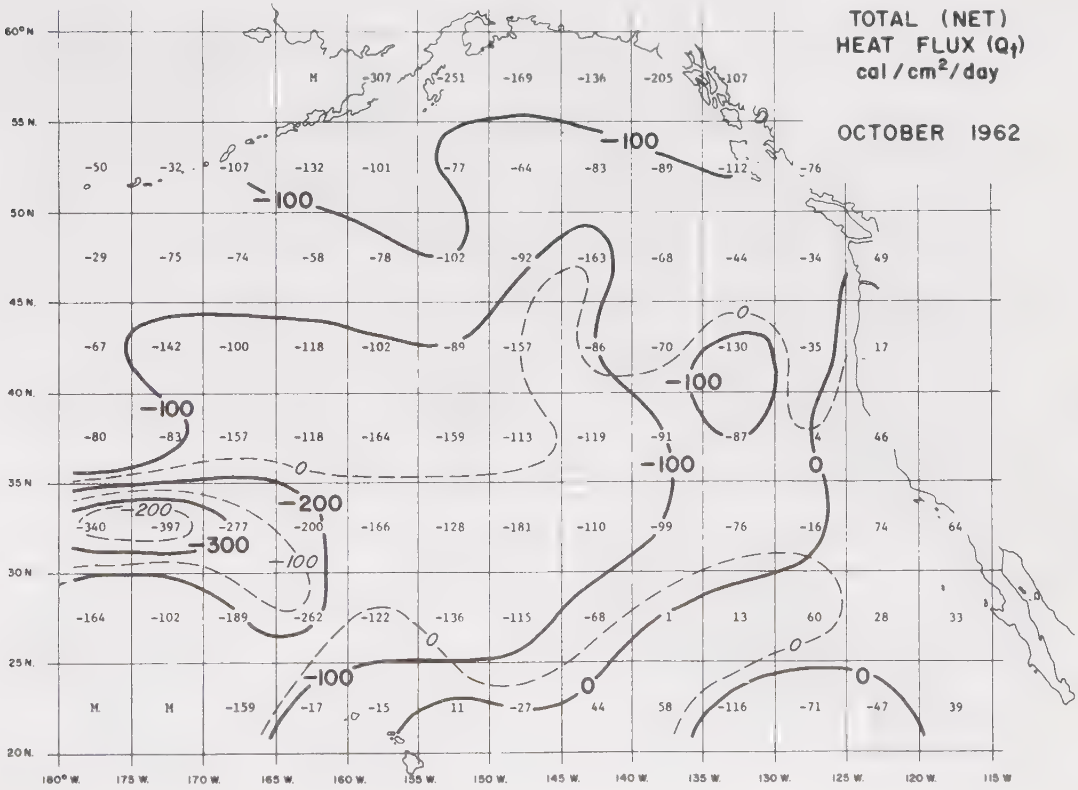


TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day

AUGUST 1962

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-217 M M 112 58 80 128
180 122 116 108 112 159 146 138 100 121 152
171 159 195 177 154 172 119 150 152 121 174 186
157 241 286 220 212 79 91 76 112 154 208 345
167 222 188 189 168 87 28 73 93 200 247 279
290 306 270 264 256 164 199 131 140 164 225 233 204
195 176 171 122 120 82 99 135 187 235 261 258 319
-208 -14 68 60 5 59 94 -81 53 188 48 253 293
+100
+200
+100
+200
+300
+100
+300
+200
+100
+100
+300
+200
0
0
0
0
0
0
0
-100


TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day
SEPTEMBER 1962
60° N
55 N.
50 N
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M -91 65 -25 -82 -72 1
49 11 -8 -28 -29 -5 23 -8 5 57 118
37 -3 -63 -7 -17 -39 8 37 -8 81 61 156
6 -98 -28 -49 -18 -53 0 83 87 100 90 227
M 43 -26 -173 -112 -10 2 84 82 124 128 112
M M 24 40 2 66 101 122 125 65 102 36 135
M M -59 159 73 32 142 129 126 143 67 38 138
M M 42 -11 -23 10 5 14 -47 -51 -59 46 -45
0
+100
-100
+100
0
+100


TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day
OCTOBER 1962
60° N
55 N.
50 N
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M -307 -251 -169 -136 -205 -107
-50 -32 -107 -132 -101 -77 -64 -83 -89 -112 -76
-29 -75 -74 -58 -78 -102 -92 -163 -68 -44 -34 49
-67 -142 -100 -118 -102 -89 -157 -86 -70 -130 -35 17
-80 -83 -157 -118 -164 -159 -113 -119 -91 -87 4 46
-340 -397 -277 -200 -166 -128 -181 -110 -99 -76 -16 74 64
-164 -102 -189 -262 -122 -136 -115 -68 1 13 60 28 33
M M -159 -17 -15 11 -27 44 58 -116 -71 -47 39
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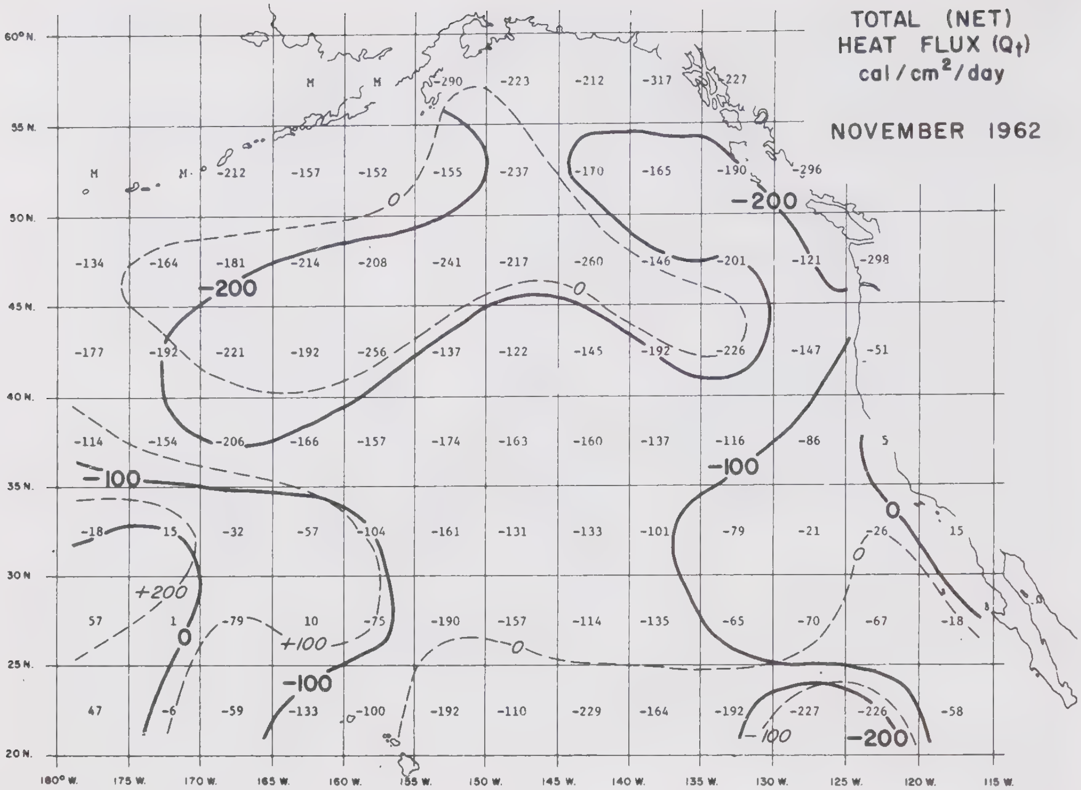
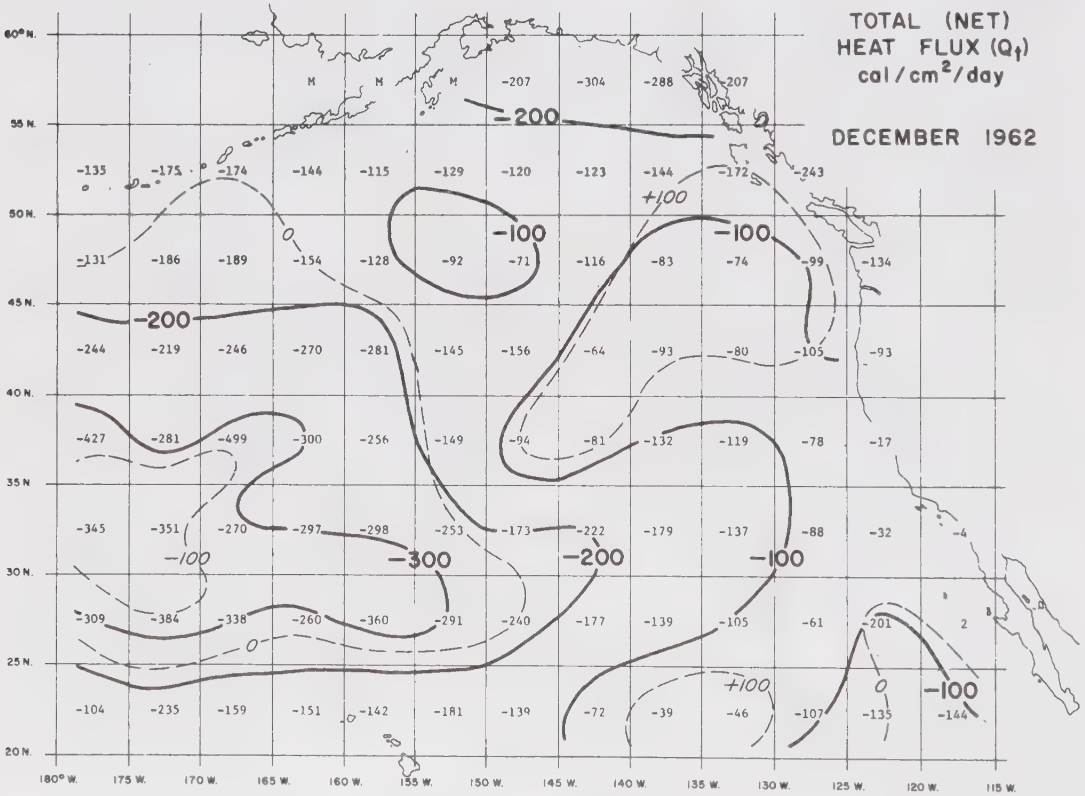
-100
-100
-100
-100
-200
-200
-300
-100
0
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t)
cal / cm^2 / day

NOVEMBER 1962

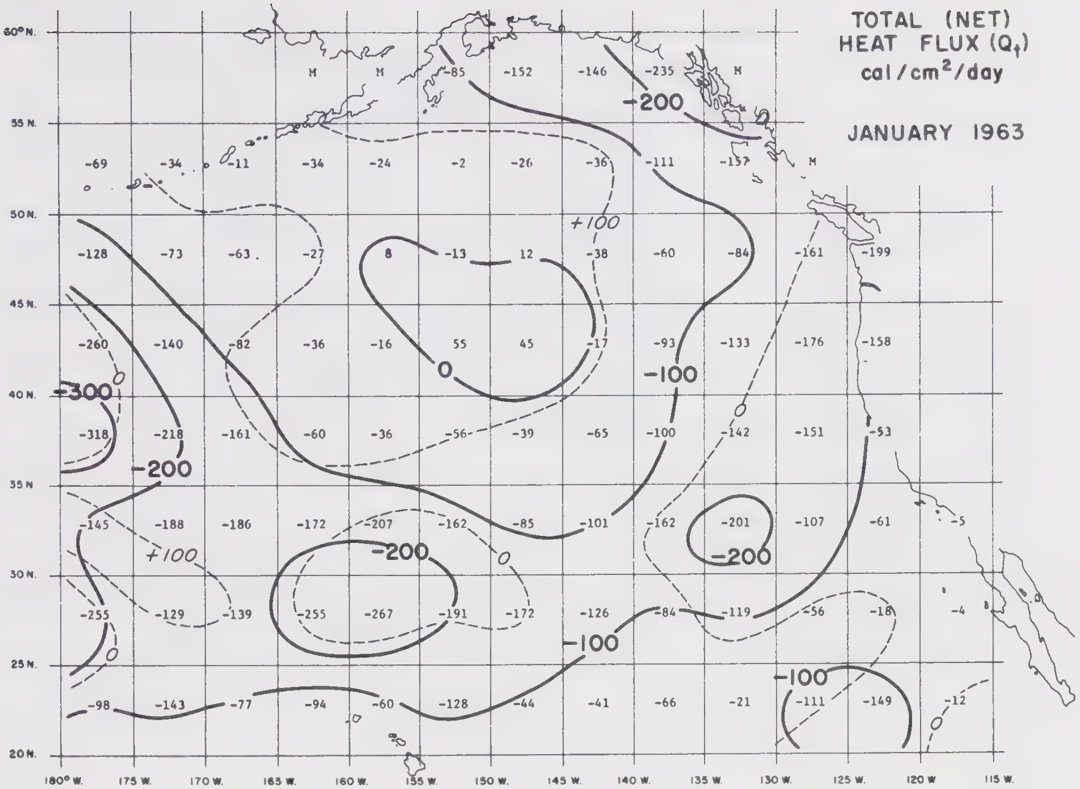
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M -290 -223 -212 -317 -227
M M -212 -157 -152 -155 -237 -170 -165 -190 -296
-134 -164 -181 -214 -208 -241 -217 -260 -146 -201 -121 -298
-177 -192 -221 -192 -256 -137 -122 -145 -192 -226 -147 -51
-114 -154 -206 -166 -157 -174 -163 -160 -137 -116 -86 5
-18 15 -32 -57 -104 -161 -131 -133 -101 -79 -21 -26 15
57 1 -79 10 -75 -190 -157 -114 -135 -65 -70 -67 -18
47 -6 -59 -133 -100 -192 -110 -229 -164 -192 -227 -226 -58
-200
-200
-200
0
0
-100
-100
+200
0
+100
-100
0
0
-100
-200

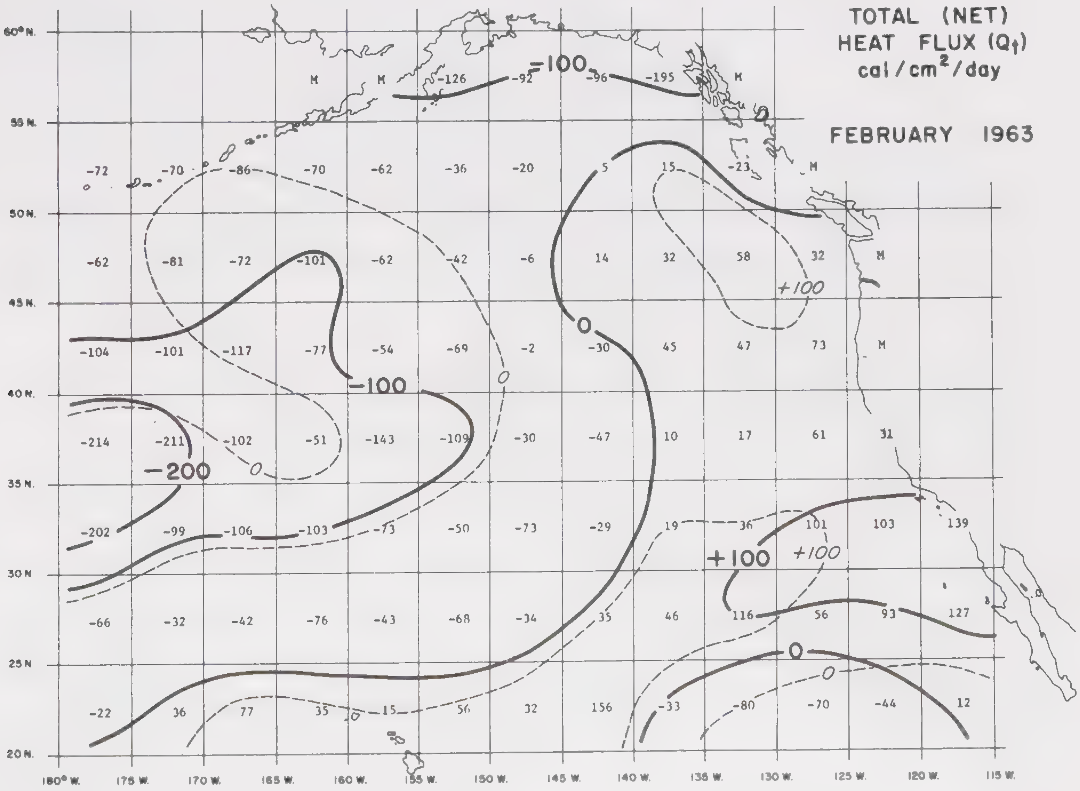


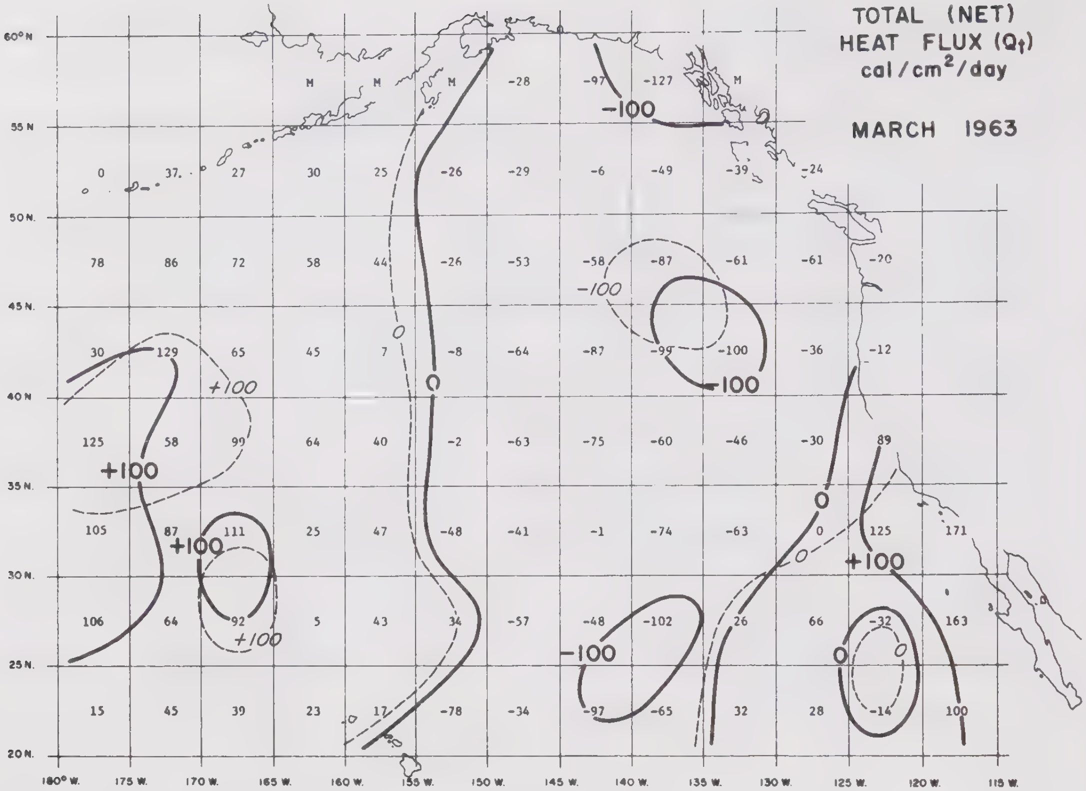
TOTAL (NET) HEAT FLUX (Q_t)
cal / cm^2 / day

DECEMBER 1962

60°N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -207 -304 -288 -207
-135 -175 -174 -144 -115 -129 -120 -123 -144 -172 -243
-131 -186 -189 -154 -128 -92 -71 -116 -83 -74 -99 -134
-244 -219 -246 -270 -281 -145 -156 -64 -93 -80 -105 -93
-427 -281 -499 -300 -256 -149 -94 -81 -132 -119 -78 -17
-345 -351 -270 -297 -298 -253 -173 -222 -179 -137 -88 -32 -4
-309 -384 -338 -260 -360 -291 -240 -177 -139 -105 -61 -201 2
-104 -235 -159 -151 -142 -181 -139 -72 -39 -46 -107 -135 -144
-200
+100
-100
-100
0
-200
-100
-300
-200
-100
0
+100
0
-100

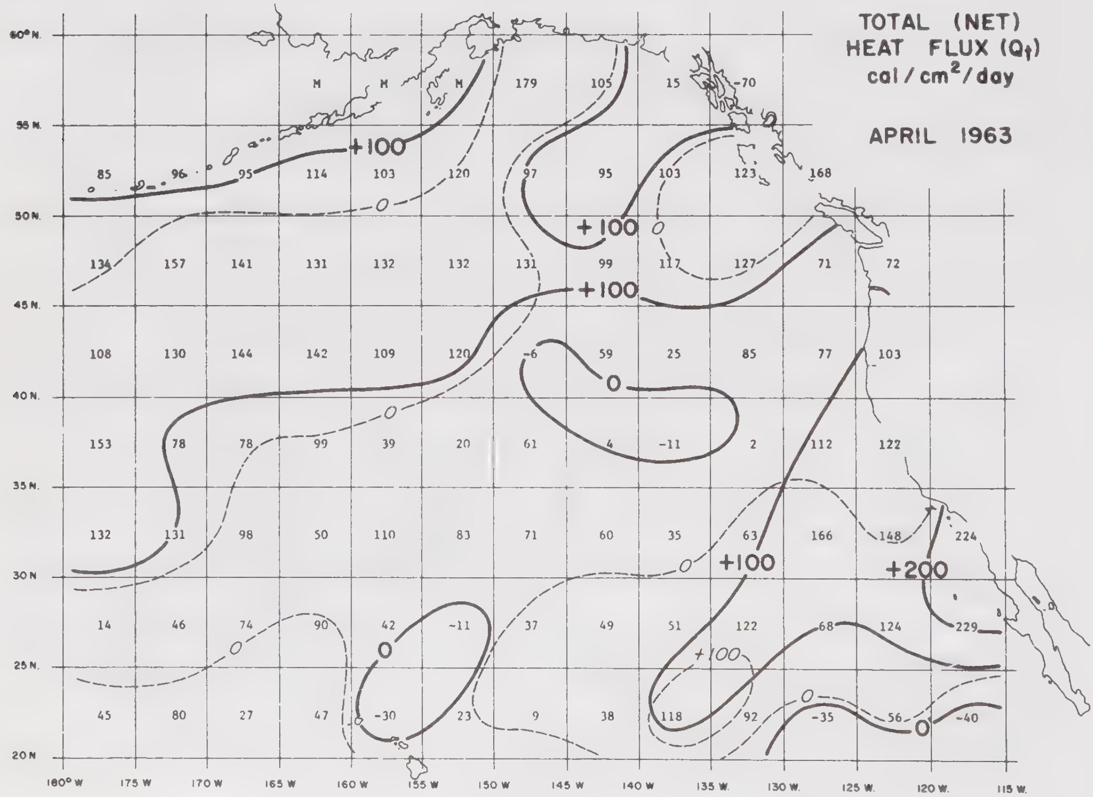

TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
JANUARY 1963
M
M
-85
-152
-146
-235
M
-200
0
M
-69
-34
-11
-34
-24
-2
-26
-36
-111
-157
+100
-128
-73
-63
-27
8
-13
12
-38
-60
-84
-161
-199
-260
-140
-82
-36
-16
55
45
-17
-93
-133
-176
-158
0
-100
-300
0
-318
-218
-161
-60
-36
-56
-39
-65
-100
-142
-151
-53
0
-200
-145
-188
-186
-172
-207
-162
-85
-101
-162
-201
-107
-61
-5
+100
-200
0
-200
-255
-129
-139
-255
-267
-191
-172
-126
-84
-119
-56
-18
-4
0
-100
-100
-98
-143
-77
-94
-60
-128
-44
-41
-66
-21
-111
-149
-12
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W
115 W.


TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
FEBRUARY 1963
M
M
-126
-92
-100
-96
-195
M
-72
-70
-86
-70
-62
-36
-20
5
15
-23
M
-62
-81
-72
-101
-62
-42
-6
14
32
58
32
M
+100
0
-104
-101
-117
-77
-54
-69
-2
-30
45
47
73
M
-100
0
-214
-211
-102
-51
-143
-109
-30
-47
10
17
61
31
-200
0
-202
-99
-106
-103
-73
-50
-73
-29
19
36
101
103
139
+100
+100
-66
-32
-42
-76
-43
-68
-34
35
46
116
56
93
127
0
0
-22
36
77
35
15
56
32
156
-33
-80
-70
-44
12
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

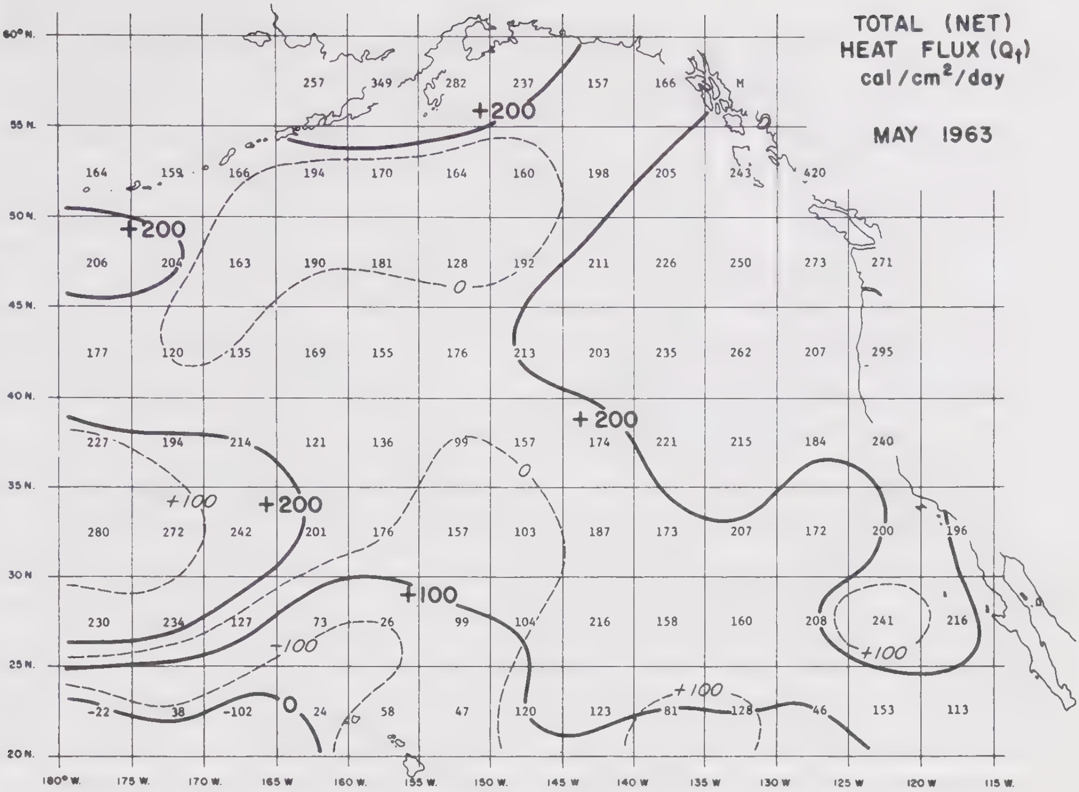
MARCH 1963

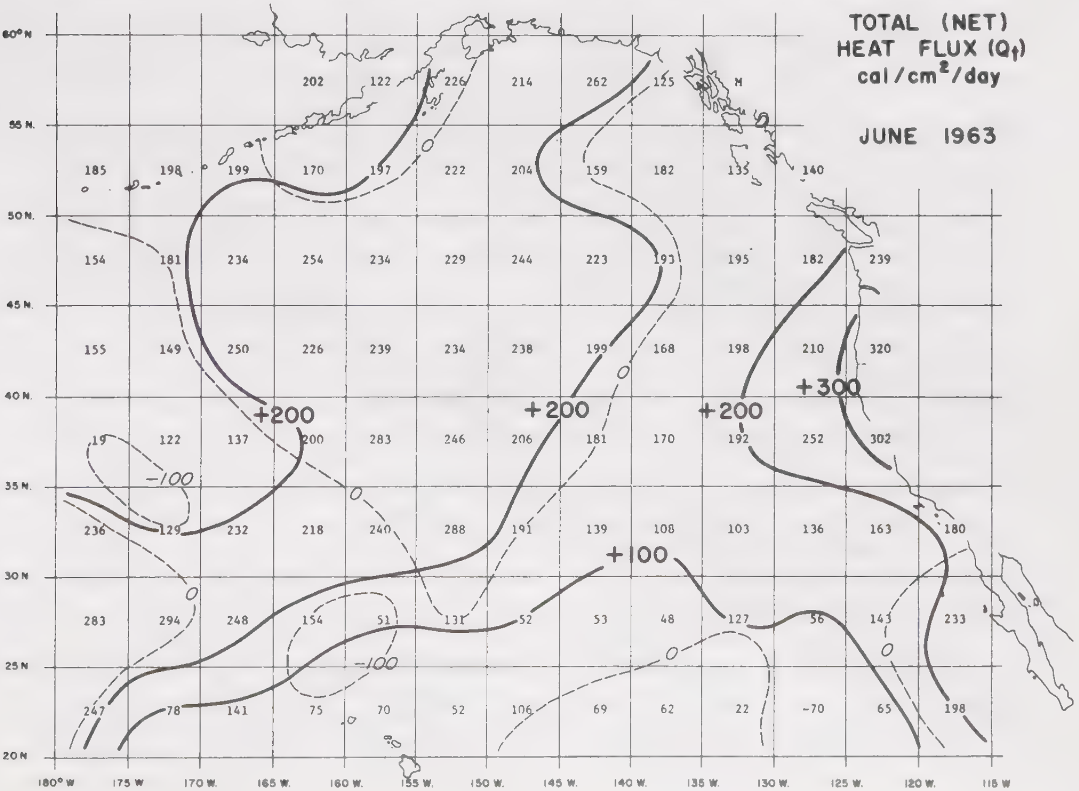
60° N
55 N
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -28 -97 -127 M
-100
0 37 27 30 25 -26 -29 -6 -49 -39 -24
78 86 72 58 44 -26 -53 -58 -87 -61 -61 -20
-100
30 129 65 45 7 -8 -64 -87 -99 -100 -36 -12
+100
0
0
-100
125 58 99 64 40 -2 -63 -75 -60 -46 -30 89
+100
0
105 87 111 25 47 -48 -41 -1 -74 -63 0 125 171
+100
0
+100
106 64 92 5 43 34 -57 -48 -102 26 66 -32 163
+100
-100
0
0
15 45 39 23 17 -78 -34 -97 -65 32 28 -14 100

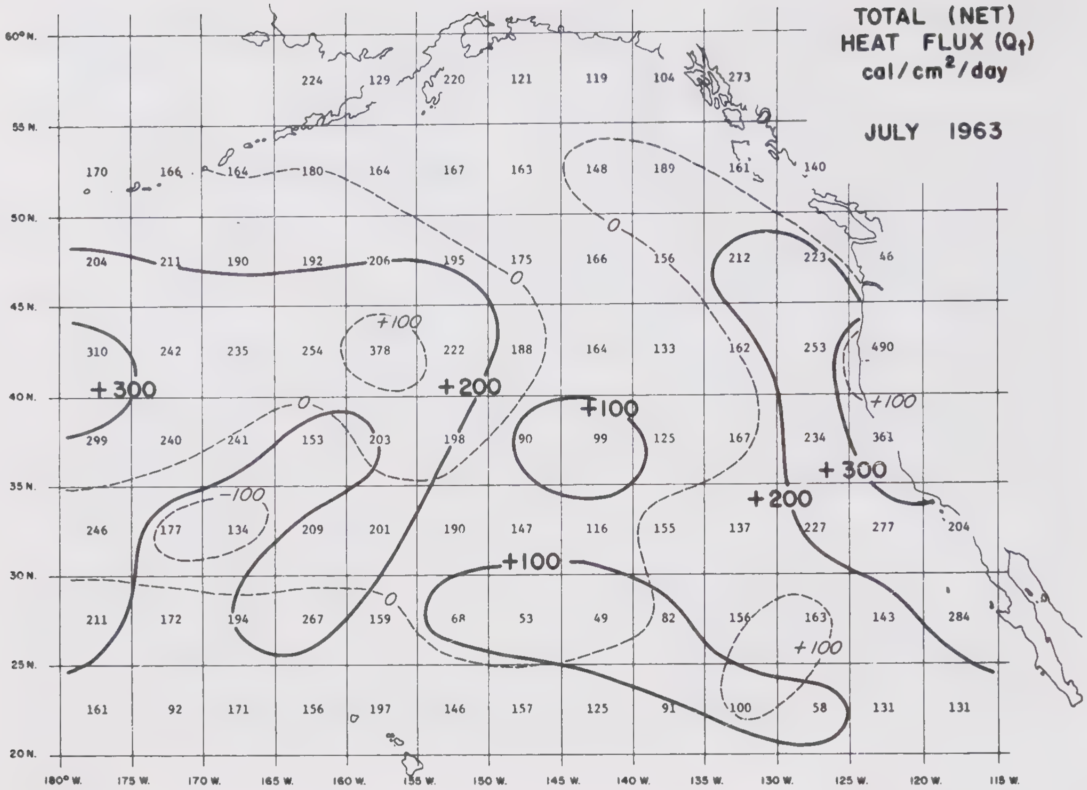

TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

APRIL 1963

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W.
130 W.
125 W.
120 W.
115 W.
M M M 179 105 15 -70
+100
85 96 95 114 103 120 97 95 103 123 168
0
+100
0
134 157 141 131 132 132 131 99 117 127 71 72
+100
108 130 144 142 109 120 -6 59 25 85 77 103
0
0
153 78 78 99 39 20 61 4 -11 2 112 122
132 131 98 50 110 83 71 60 35 63 166 148 224
0
+100
+200
14 46 74 90 42 -11 37 49 51 122 68 124 229
0
0
+100
45 80 27 47 -30 23 9 38 118 92 -35 56 -40
0
0


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm^2/day
MAY 1963
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W
160 W.
155 W.
150 W.
145 W
140 W
135 W
130 W
125 W
120 W
115 W.
M
257 349 282 237 157 166
164 159 166 194 170 164 160 198 205 243 420
206 204 163 190 181 128 192 211 226 250 273 271
177 120 135 169 155 176 213 203 235 262 207 295
227 194 214 121 136 99 157 174 221 215 184 240
280 272 242 201 176 157 103 187 173 207 172 200 196
230 234 127 73 26 99 104 216 158 160 208 241 216
-22 38 -102 24 58 47 120 123 81 128 46 153 113
+200
+200
+200
+200
+100
+100
+100
+100
-100
0
0
0

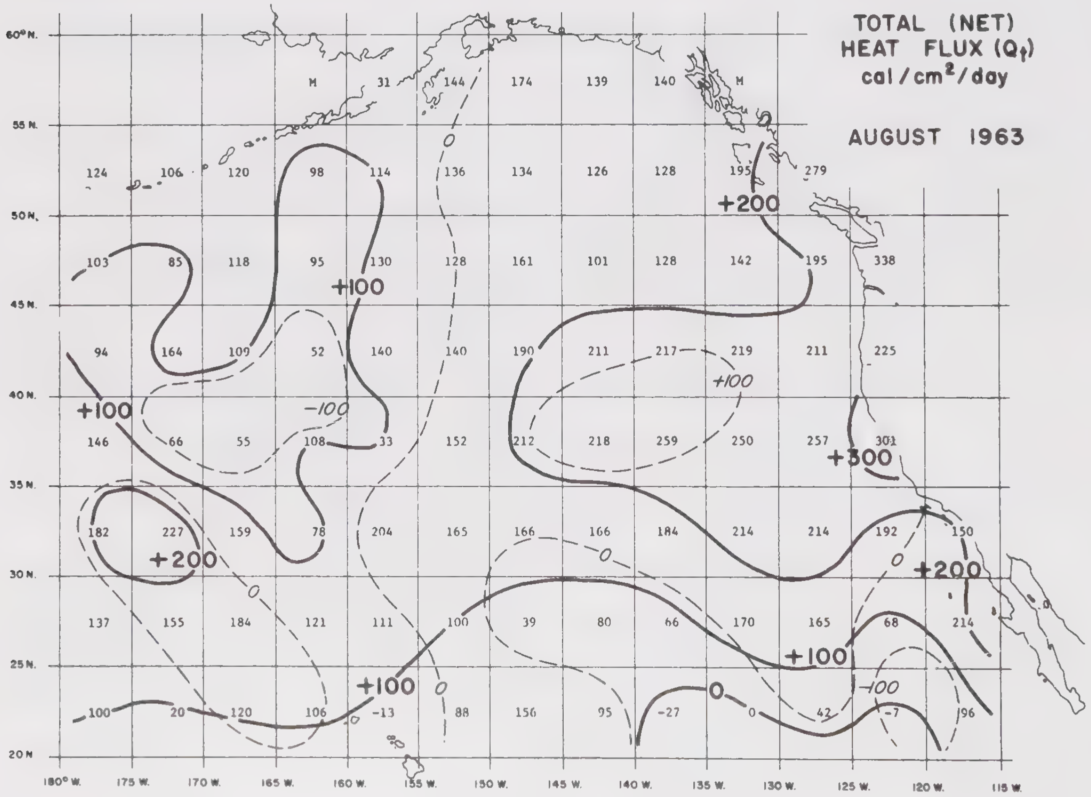

TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm^2/day
JUNE 1963
60° N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N
180° W
175 W
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M
202 122 226 214 262 125
185 198 199 170 197 222 204 159 182 135 140
154 181 234 254 234 229 244 223 193 195 182 239
155 149 250 226 239 234 238 199 168 198 210 320
19 122 137 200 283 246 206 181 170 192 252 302
236 129 232 218 240 288 191 139 108 103 136 163 180
283 294 248 154 51 131 52 53 48 127 56 143 233
247 78 141 75 70 52 106 69 62 22 -70 65 198
+200
+200
+200
+300
+100
-100
-100
0
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JULY 1963

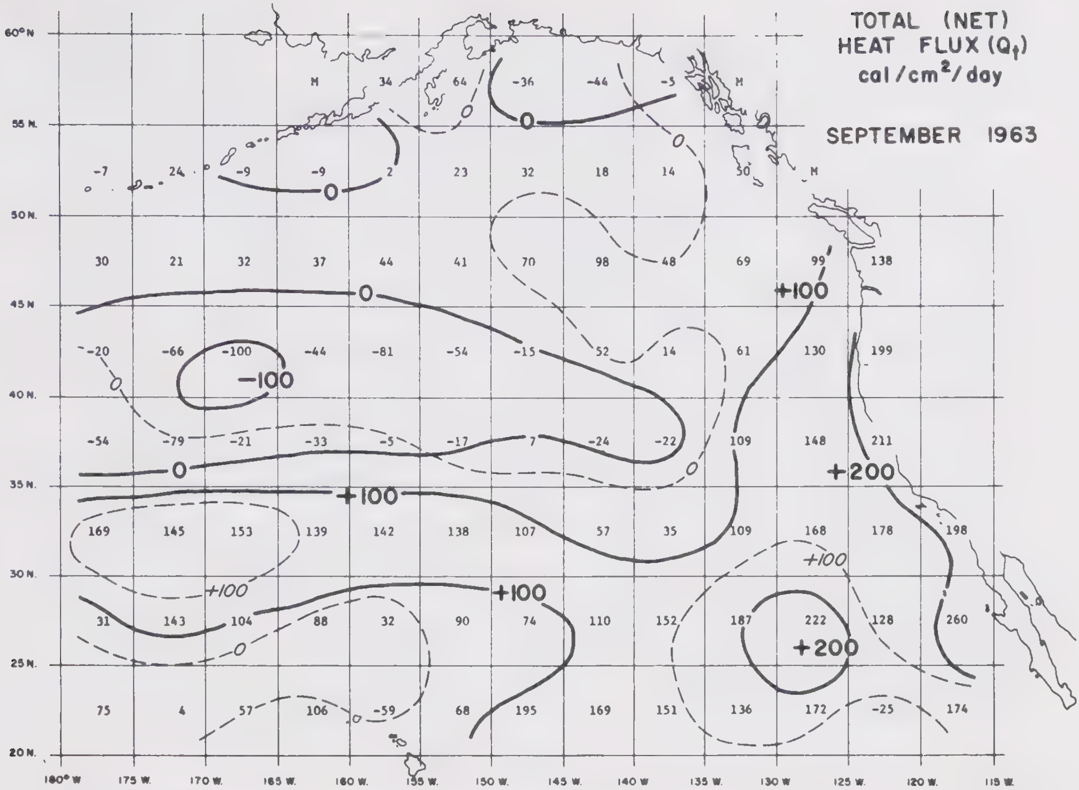
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
224 129 220 121 119 104 273
170 166 164 180 164 167 163 148 189 161 140
204 211 190 192 206 195 175 166 156 212 223 46
310 242 235 254 378 222 188 164 133 162 253 490
299 240 241 153 203 198 90 99 125 167 234 361
246 177 134 209 201 190 147 116 155 137 227 277 204
211 172 194 267 159 68 53 49 82 156 163 143 284
161 92 171 156 197 146 157 125 91 100 58 131 131
+300
+100
+200
0
0
0
+100
-100
+100
+300
+200
+100
0
+100



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

AUGUST 1963

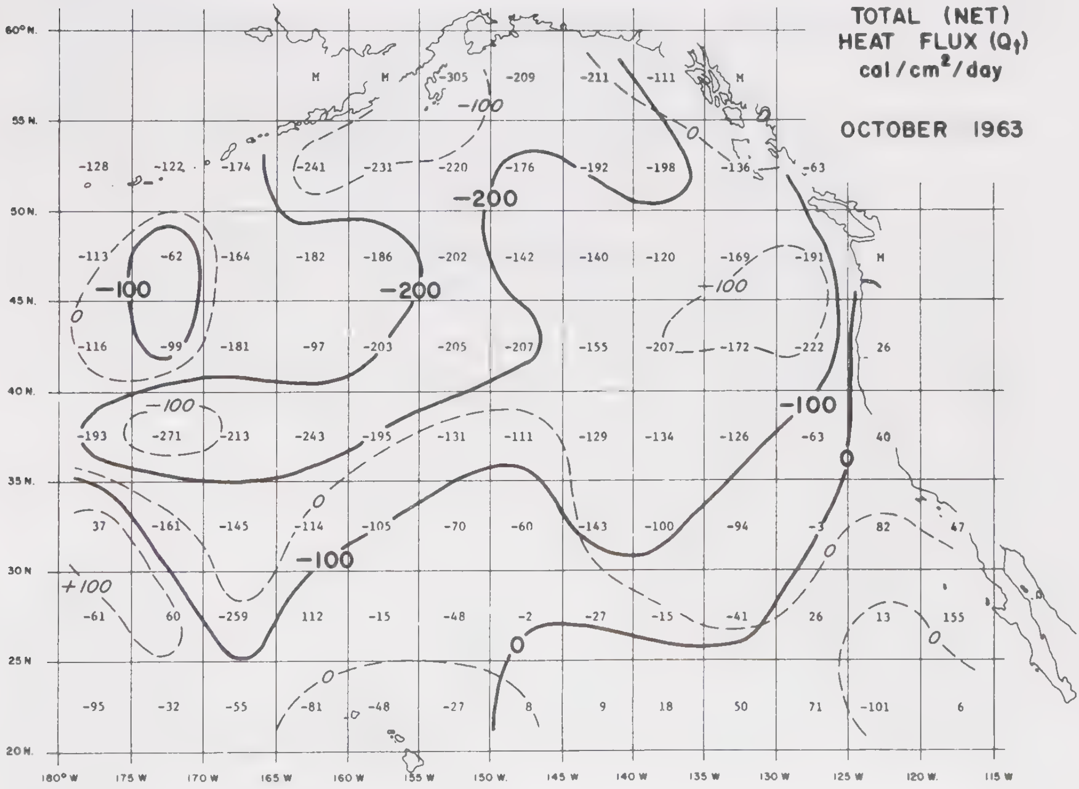
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M 31 144 174 139 140 M
124 106 120 98 114 136 134 126 128 195 279
103 85 118 95 130 128 161 101 128 142 195 338
94 164 109 52 140 140 190 211 217 219 211 225
146 66 55 108 33 152 212 218 259 250 257 301
182 227 159 78 204 165 166 166 184 214 214 192 150
137 155 184 121 111 100 39 80 66 170 165 68 214
100 20 120 106 -13 88 156 95 -27 0 42 -7 96
0
+200
+100
+100
+100
-100
+300
+200
0
0
+200
+100
+100
0
0
-100



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

SEPTEMBER 1963

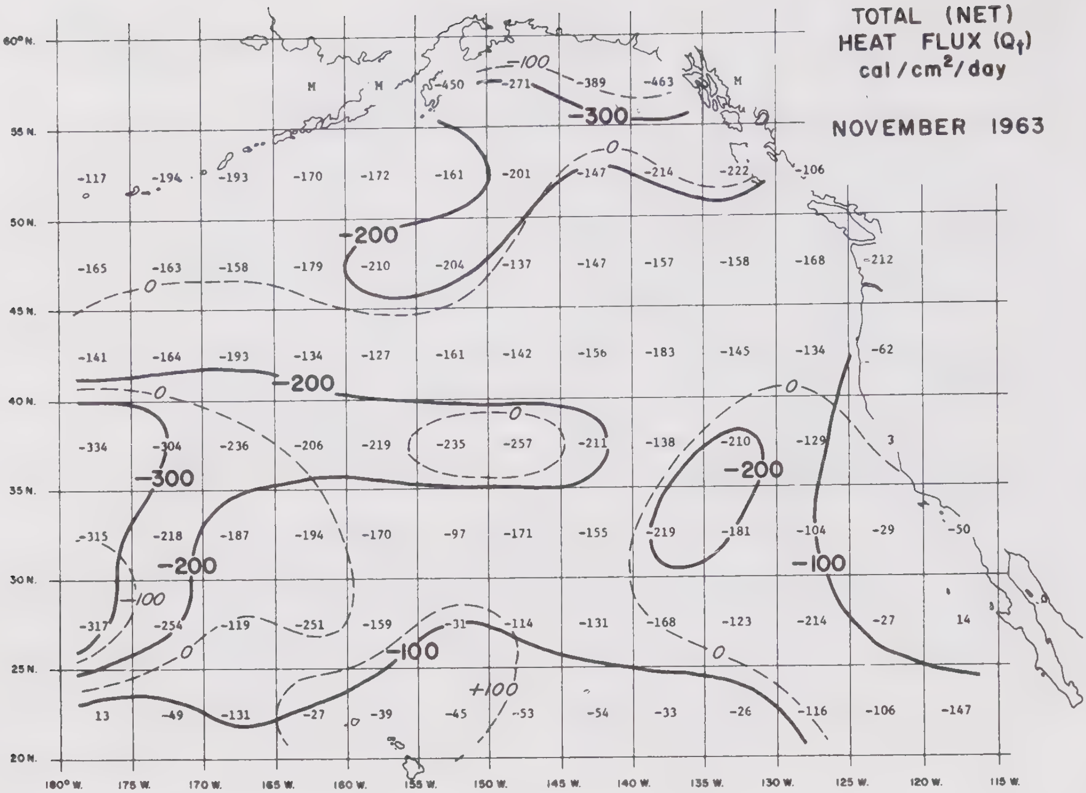
60° N
55 N.
50 N.
45 N
40 N.
35 N.
30 N.
25 N.
20 N.
180° W
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M 34 64 -36 -44 -5 M
-7 24 -9 -9 2 23 32 18 14 50 M
30 21 32 37 44 41 70 98 48 69 99 138
-20 -66 -100 -44 -81 -54 -15 52 14 61 130 199
-54 -79 -21 -33 -5 -17 7 -24 -22 109 148 211
169 145 153 139 142 138 107 57 35 109 168 178 198
31 143 104 88 32 90 74 110 152 187 222 128 260
75 4 57 106 -59 68 195 169 151 136 172 -25 174
0
0
0
0
-100
0
+100
+100
+200
+100
+100
+100
0
+200
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

OCTOBER 1963

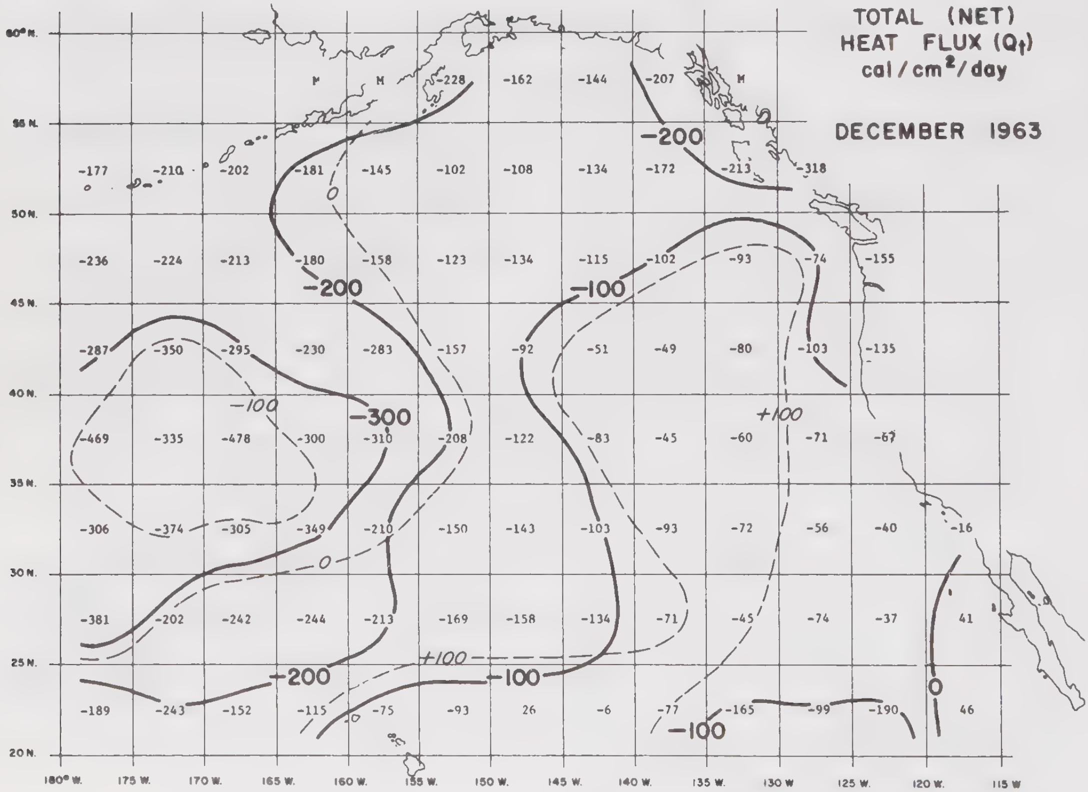
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N.
180° W
175 W
170 W
165 W
160 W
155 W
150 W.
145 W
140 W
135 W.
130 W
125 W
120 W.
115 W
M M -305 -209 -211 -111 M
-128 -122 -174 -241 -231 -220 -176 -192 -198 -136 -63
-113 -62 -164 -182 -186 -202 -142 -140 -120 -169 -191 M
-116 -99 -181 -97 -203 -205 -207 -155 -207 -172 -222 26
-193 -271 -213 -243 -195 -131 -111 -129 -134 -126 -63 40
37 -161 -145 -114 -105 -70 -60 -143 -100 -94 -3 82 47
-61 60 -259 112 -15 -48 -2 -27 -15 -41 26 13 155
-95 -32 -55 -81 -48 -27 8 9 18 50 71 -101 6
-100
0
-200
-100
-200
0
-100
+100
-100
0
-100
0
+100
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

NOVEMBER 1963

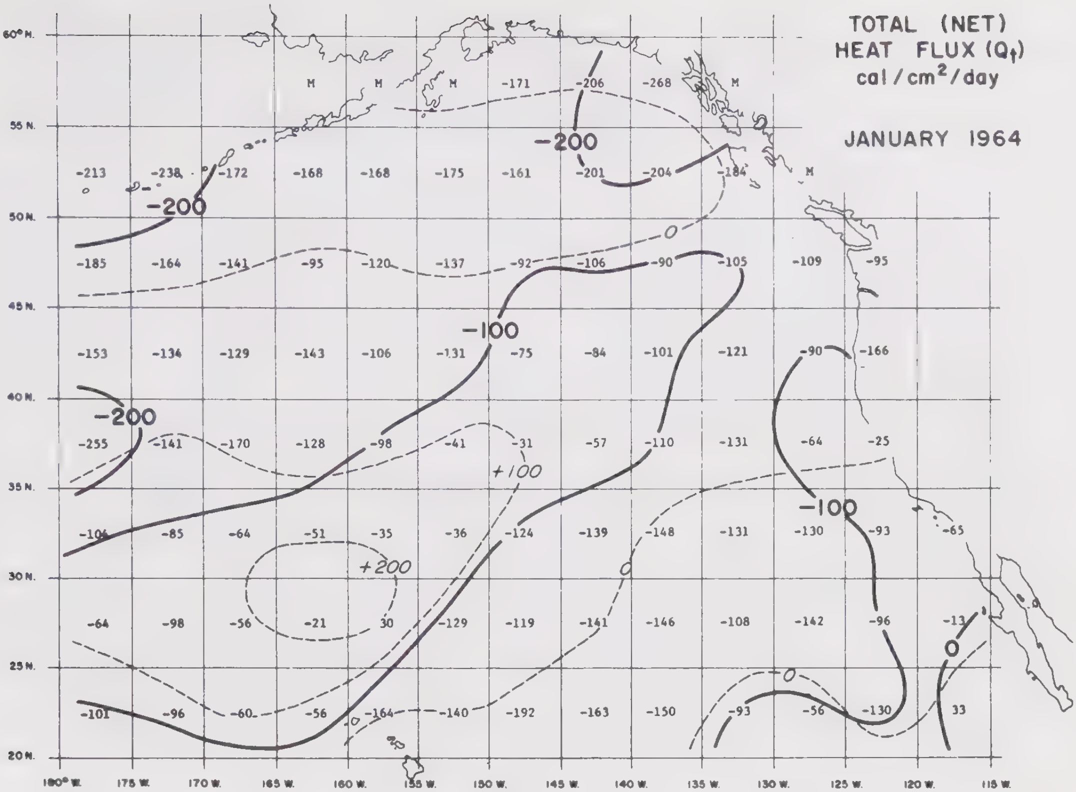
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
M
-450
-271
-389
-463
M
-100
-300
-117
-194
-193
-170
-172
-161
-201
-147
-214
-222
-106
0
-200
-165
-163
-158
-179
-210
-204
-137
-147
-157
-158
-168
-212
0
-141
-164
-193
-134
-127
-161
-142
-156
-183
-145
-134
-62
-200
0
0
0
-334
-304
-236
-206
-219
-235
-257
-211
-138
-210
-129
3
-300
-200
-315
-218
-187
-194
-170
-97
-171
-155
-219
-181
-104
-29
-50
-200
-100
-100
-317
-254
-119
-251
-159
-31
-114
-131
-168
-123
-214
-27
14
0
-100
0
+100
13
-49
-131
-27
-39
-45
-53
-54
-33
-26
-116
-106
-147



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

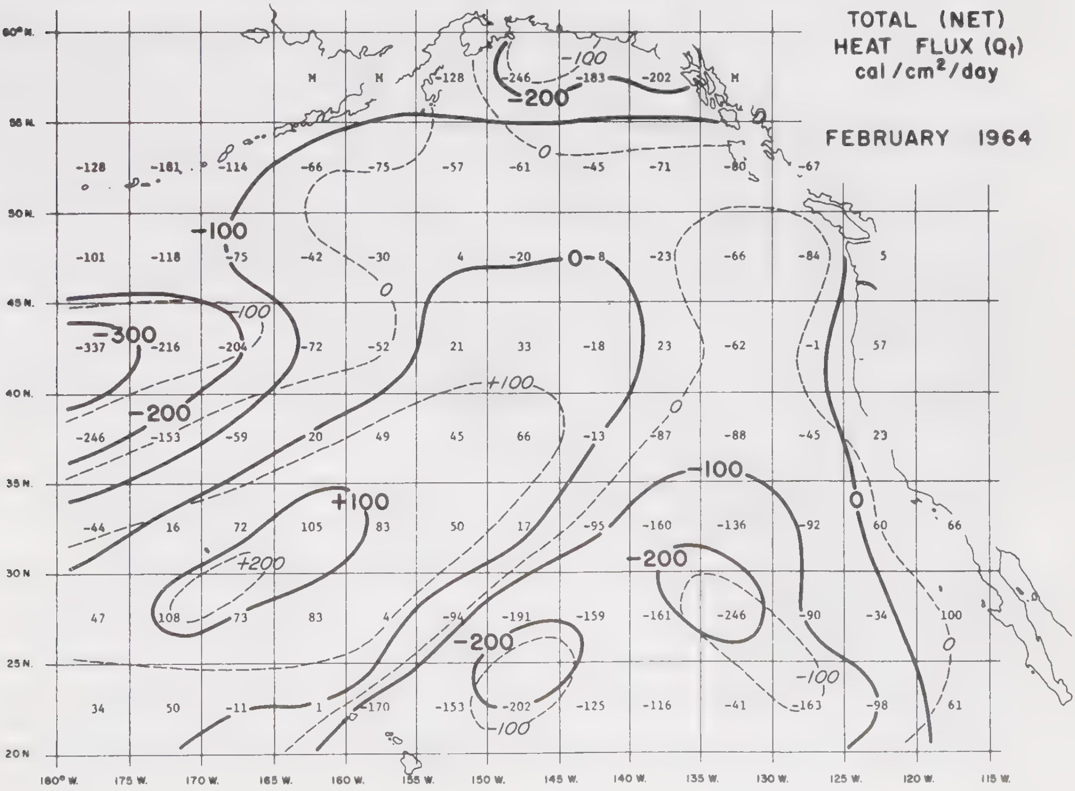
DECEMBER 1963

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
M
-228
-162
-144
-207
M
-200
-177
-210
-202
-181
-145
-102
-108
-134
-172
-213
-318
0
-236
-224
-213
-180
-158
-123
-134
-115
-102
-93
-74
-155
-200
-100
-287
-350
-295
-230
-283
-157
-92
-51
-49
-80
-103
-135
-100
-300
+100
-469
-335
-478
-300
-310
-208
-122
-83
-45
-60
-71
-67
-306
-374
-305
-349
-210
-150
-143
-103
-93
-72
-56
-40
-16
0
-381
-202
-242
-244
-213
-169
-158
-134
-71
-45
-74
-37
41
+100
-200
-100
0
-189
-243
-152
-115
-75
-93
26
-6
-77
-165
-99
-190
46
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

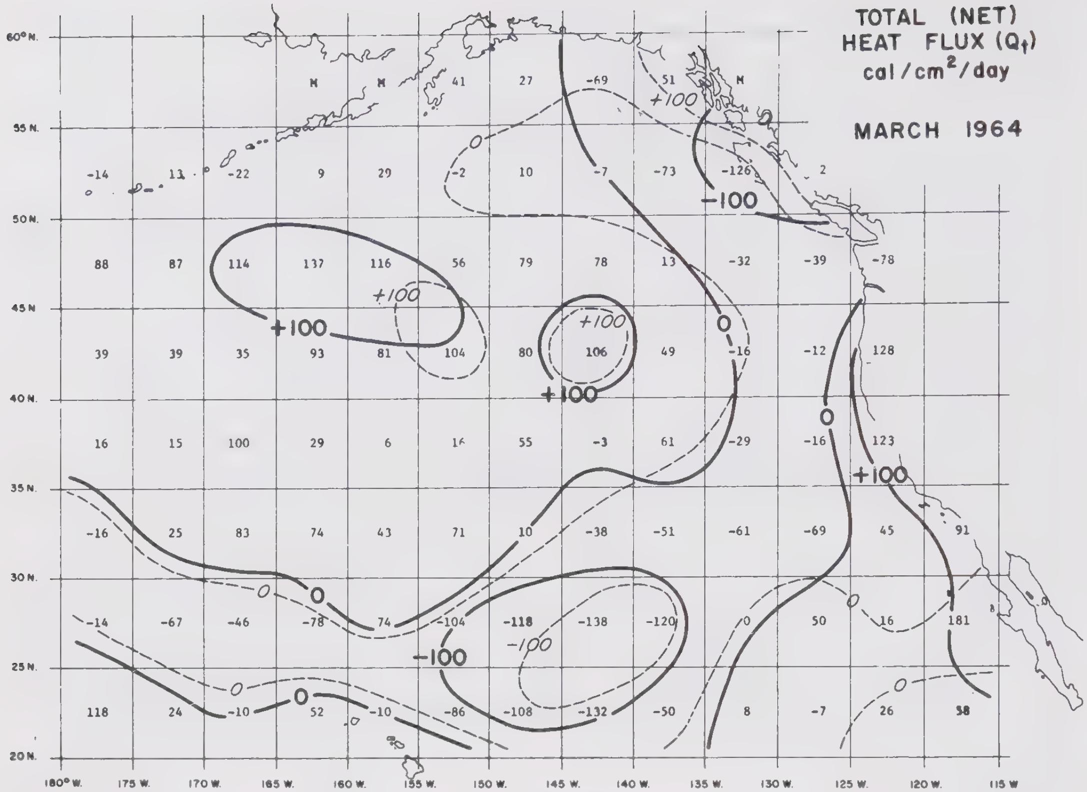
JANUARY 1964

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -171 -206 -268 M
-213 -238 -172 -168 -168 -175 -161 -201 -204 -184 M
-185 -164 -141 -95 -120 -137 -92 -106 -90 -105 -109 -95
-153 -134 -129 -143 -106 -131 -75 -84 -101 -121 -90 -166
-255 -141 -170 -128 -98 -41 -31 -57 -110 -131 -64 -25
-106 -85 -64 -51 -35 -36 -124 -139 -148 -131 -130 -93 -65
-64 -98 -56 -21 30 -129 -119 -141 -146 -108 -142 -96 -13
-101 -96 -60 -56 -164 -140 -192 -163 -150 -93 -56 -130 33
-200
-200
-200
-100
+100
+200
0
-100
0
0
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

FEBRUARY 1964

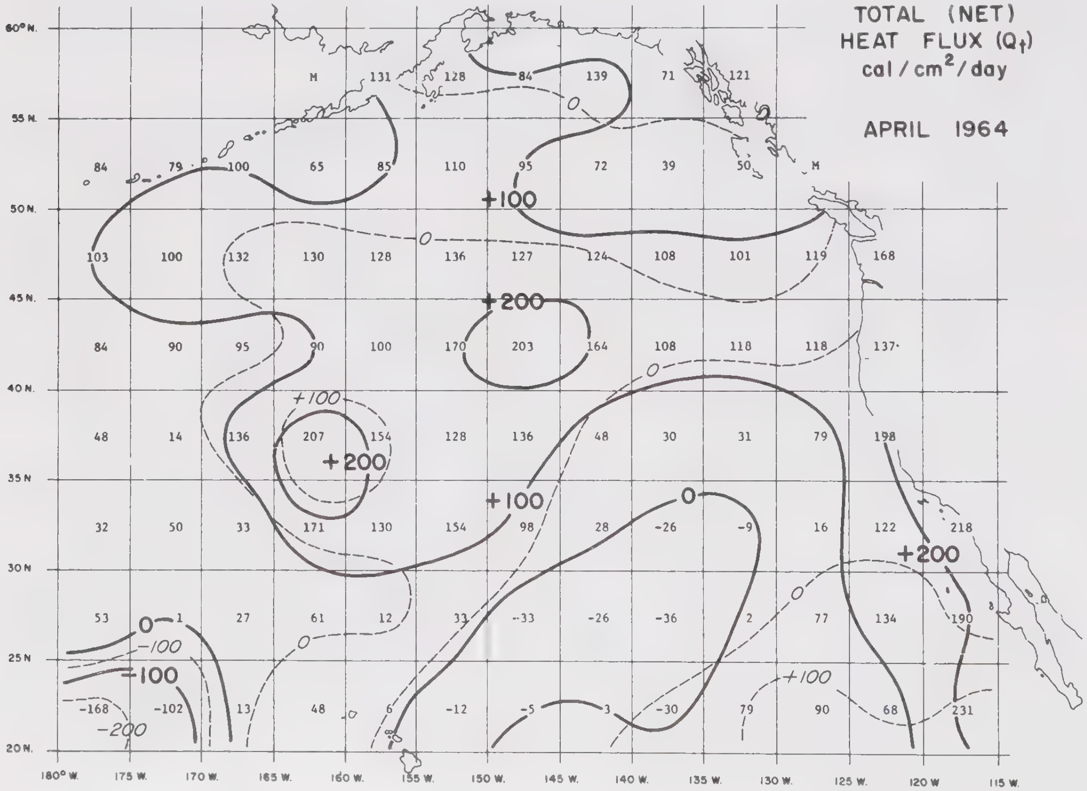
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M -128 -246 -183 -202 M
-128 -181 -114 -66 -75 -57 -61 -45 -71 -80 -67
-101 -118 -75 -42 -30 4 -20 8 -23 -66 -84 5
-337 -216 -204 -72 -52 21 33 -18 23 -62 -1 57
-246 -153 -59 20 49 45 66 -13 -87 -88 -45 23
-44 16 72 105 83 50 17 -95 -160 -136 -92 60 66
47 108 73 83 4 -94 -191 -159 -161 -246 -90 -34 100
34 50 -11 1 -170 -153 -202 -125 -116 -41 -163 -98 61
-100
-200
0
-100
0
-300
-100
-200
+100
+100
+200
-100
-200
-200
-100
-100
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day

MARCH 1964

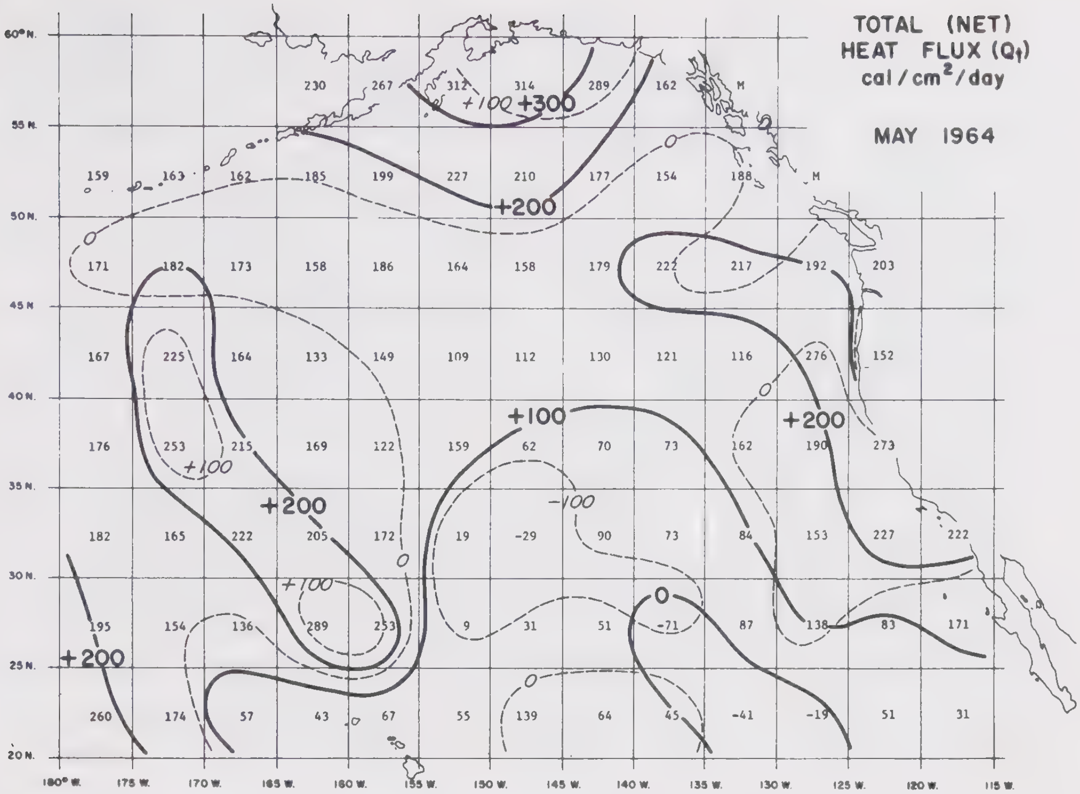
60° N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
+100
-100
0



TOTAL (NET) HEAT FLUX (Q_t) cal / cm^2 / day

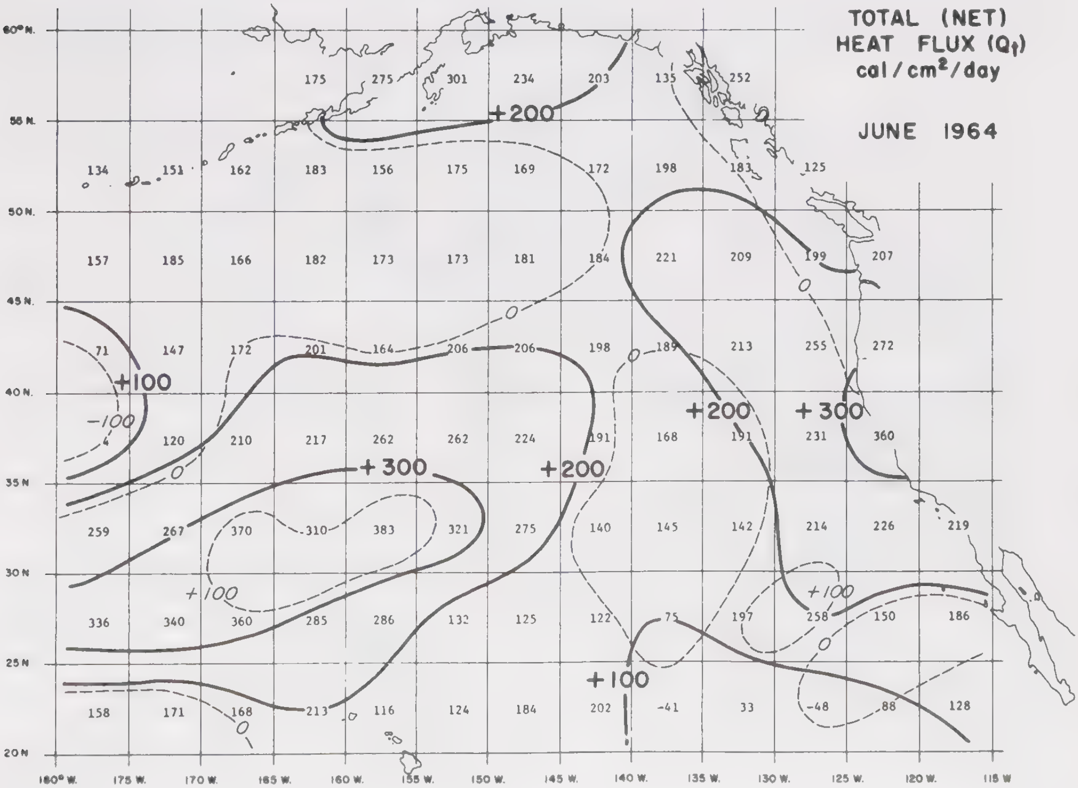
APRIL 1964

60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W
115 W.
+100
+200
0
-100
-200


60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
230 267 312 314 289 162 M
+100 +300
159 163 162 185 199 227 210 177 154 188 M
0
+200
171 182 173 158 186 164 158 179 222 217 192 203
167 225 164 133 149 109 112 130 121 116 276 152
0
+100 +200
176 253 215 169 122 159 62 70 73 162 190 273
+100
+200 -100
182 165 222 205 172 19 -29 90 73 84 153 227 222
0
+100 0
195 154 136 289 253 9 31 51 -71 87 138 83 171
+200
0
260 174 57 43 67 55 139 64 45 -41 -19 51 31
180° W. 175 W. 170 W. 165 W. 160 W. 155 W. 150 W. 145 W. 140 W. 135 W. 130 W. 125 W. 120 W. 115 W.

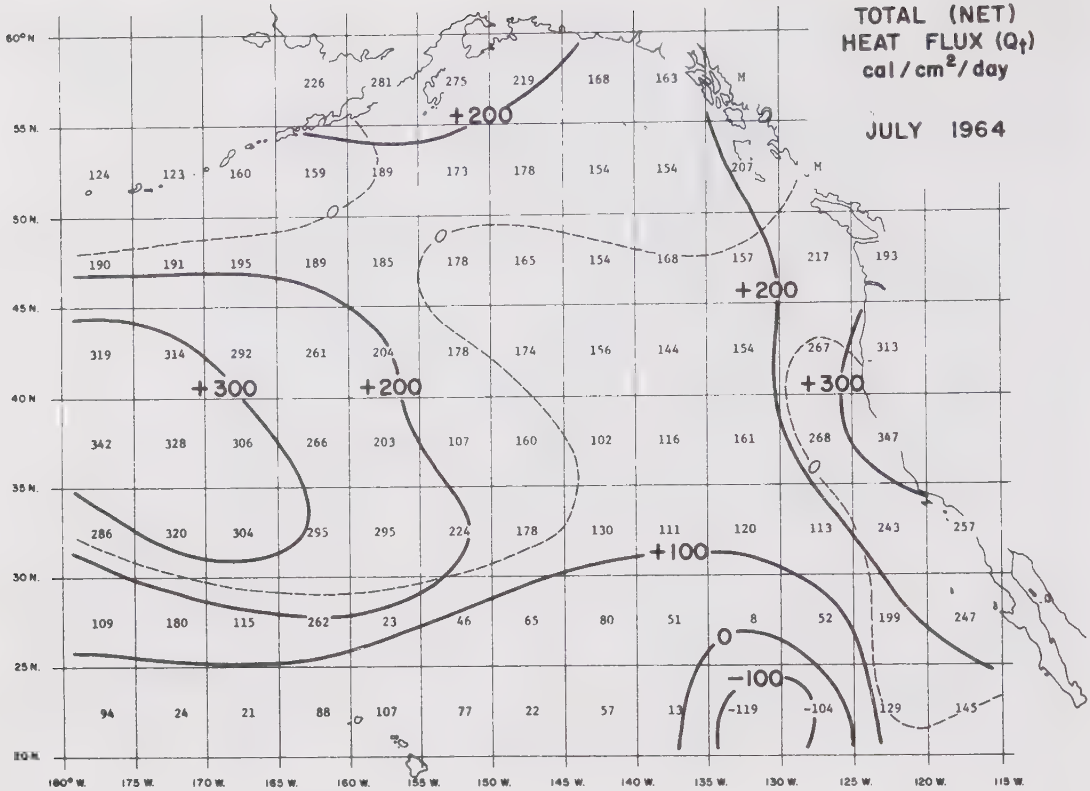
TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm^2/day

MAY 1964


60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
175 275 301 234 203 135 252
+200
134 151 162 183 156 175 169 172 198 183 125
157 185 166 182 173 173 181 184 221 209 199 207
0
0
0
71 147 172 201 164 206 206 198 189 213 255 272
+100
+200 +300
-100
4 120 210 217 262 262 224 191 168 191 231 360
0
+300 +200
259 267 370 310 383 321 275 140 145 142 214 226 219
+100 +100
336 340 360 285 286 132 125 122 75 197 258 150 186
0
+100
158 171 168 213 116 124 184 202 -41 33 -48 88 128
0
180° W. 175 W. 170 W. 165 W. 160 W. 155 W. 150 W. 145 W. 140 W. 135 W. 130 W. 125 W. 120 W. 115 W.

TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm^2/day

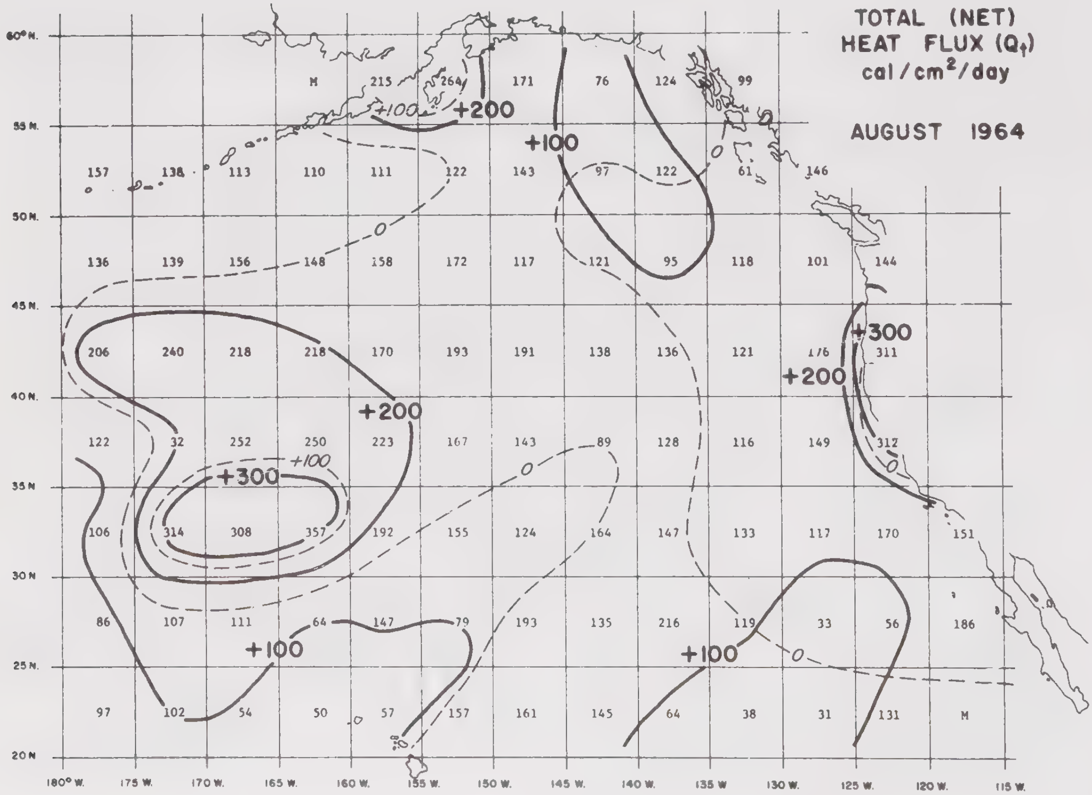
JUNE 1964



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

JULY 1964

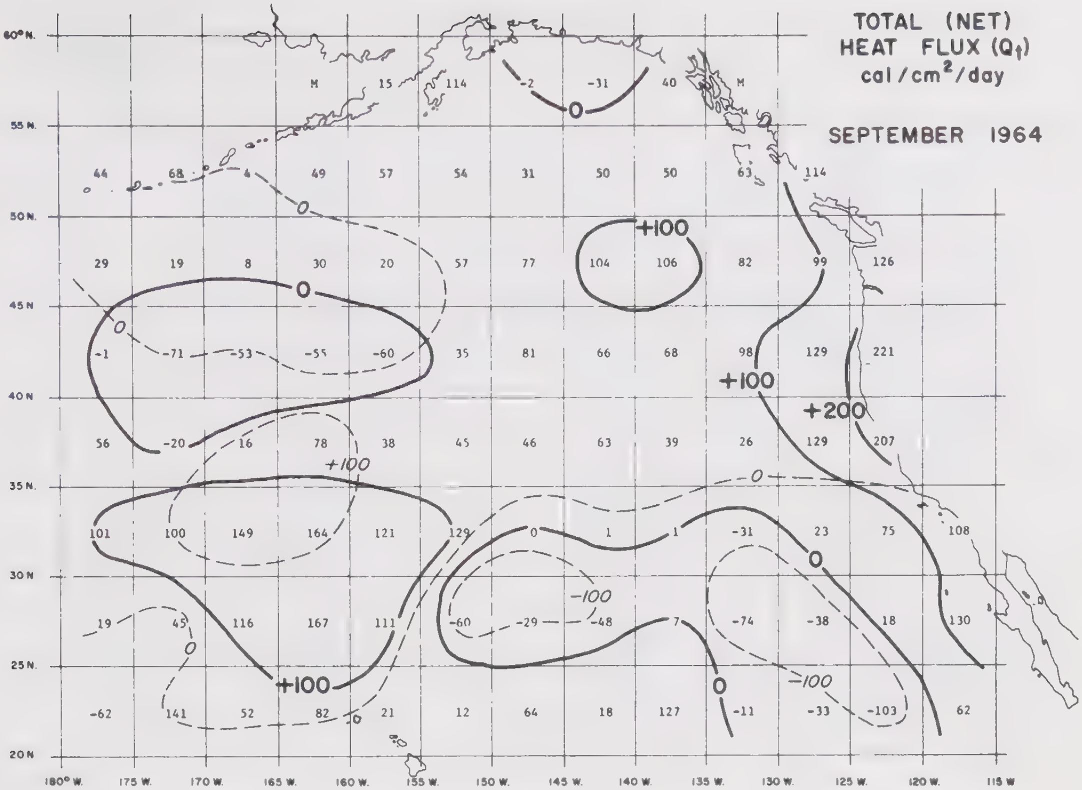
60° N
55 N.
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
226 281 275 219 168 163 M
+200
124 123 160 159 189 173 178 154 154 207 M
0
190 191 195 189 185 178 165 154 168 157 217 193
+200
319 314 292 261 204 178 174 156 144 154 267 313
+300 +200 +300
342 328 306 266 203 107 160 102 116 161 268 347
0
286 320 304 295 295 224 178 130 111 120 113 243 257
+100
109 180 115 262 23 46 65 80 51 8 52 199 247
0
-100
94 24 21 88 107 77 22 57 13 -119 -104 129 145

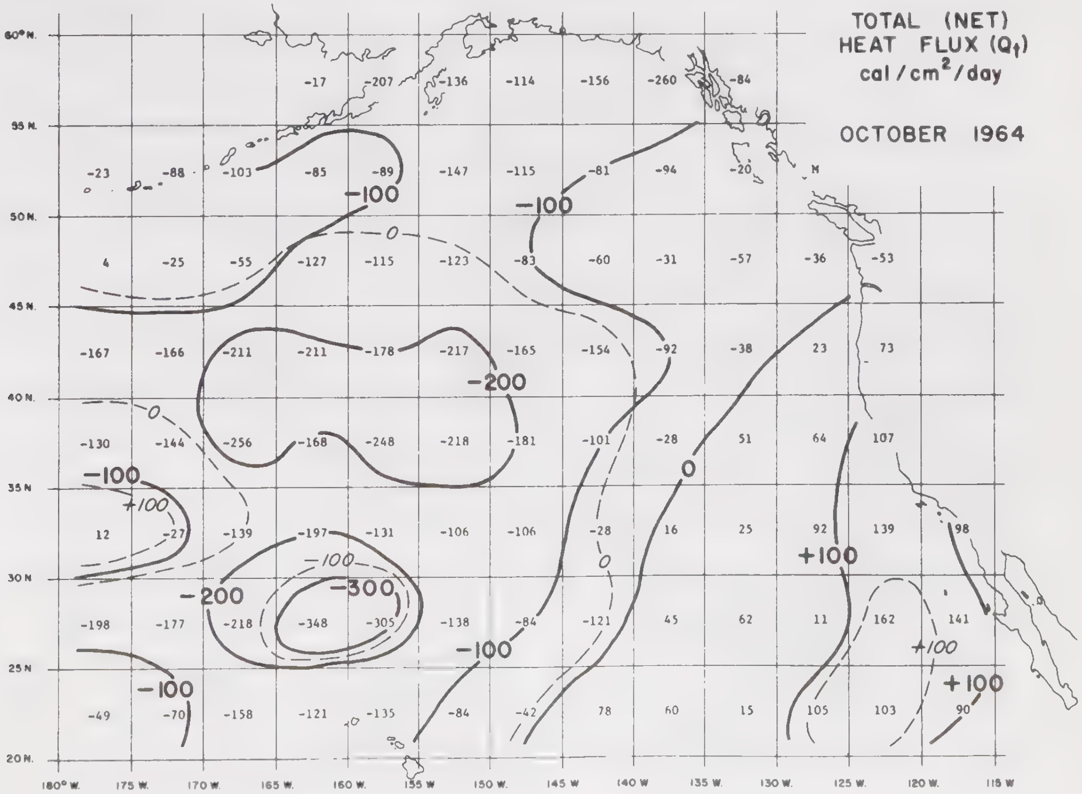


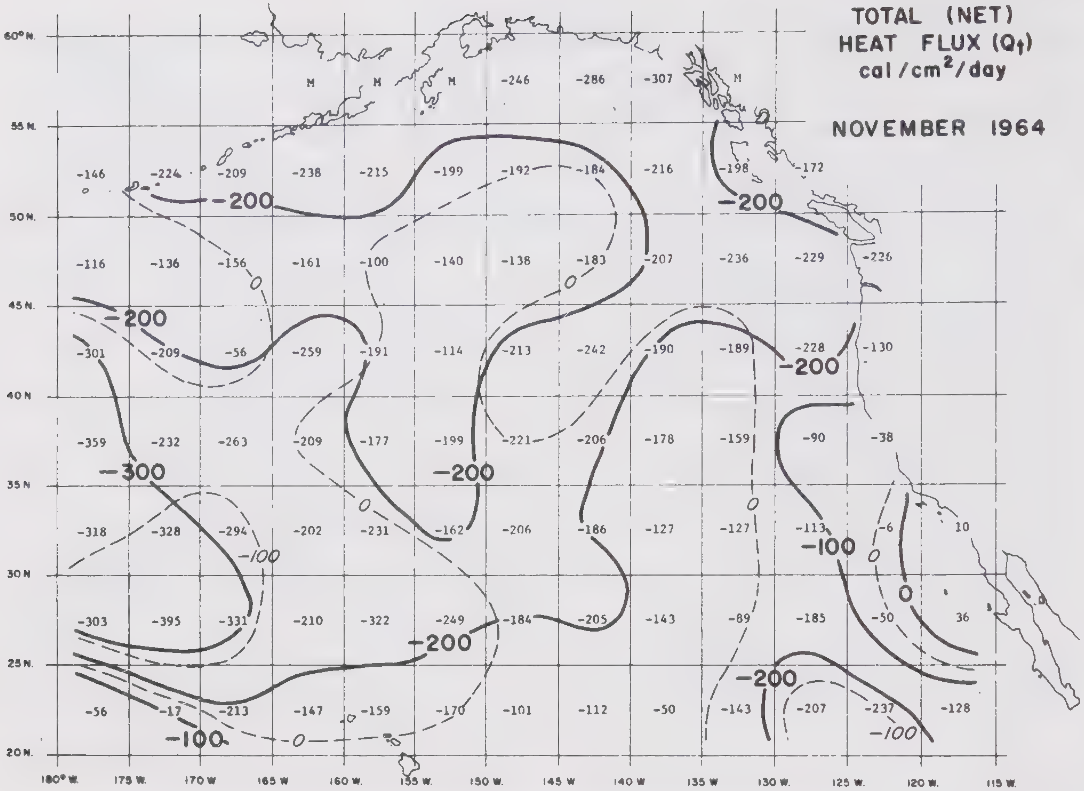
TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

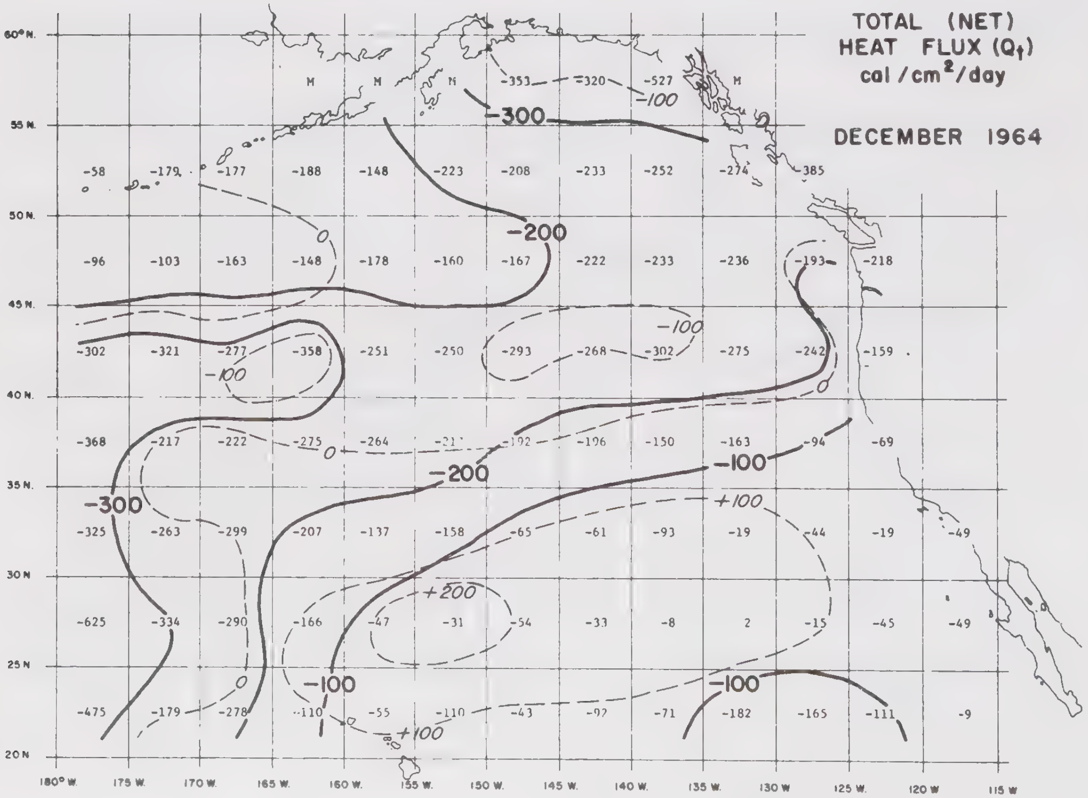
AUGUST 1964

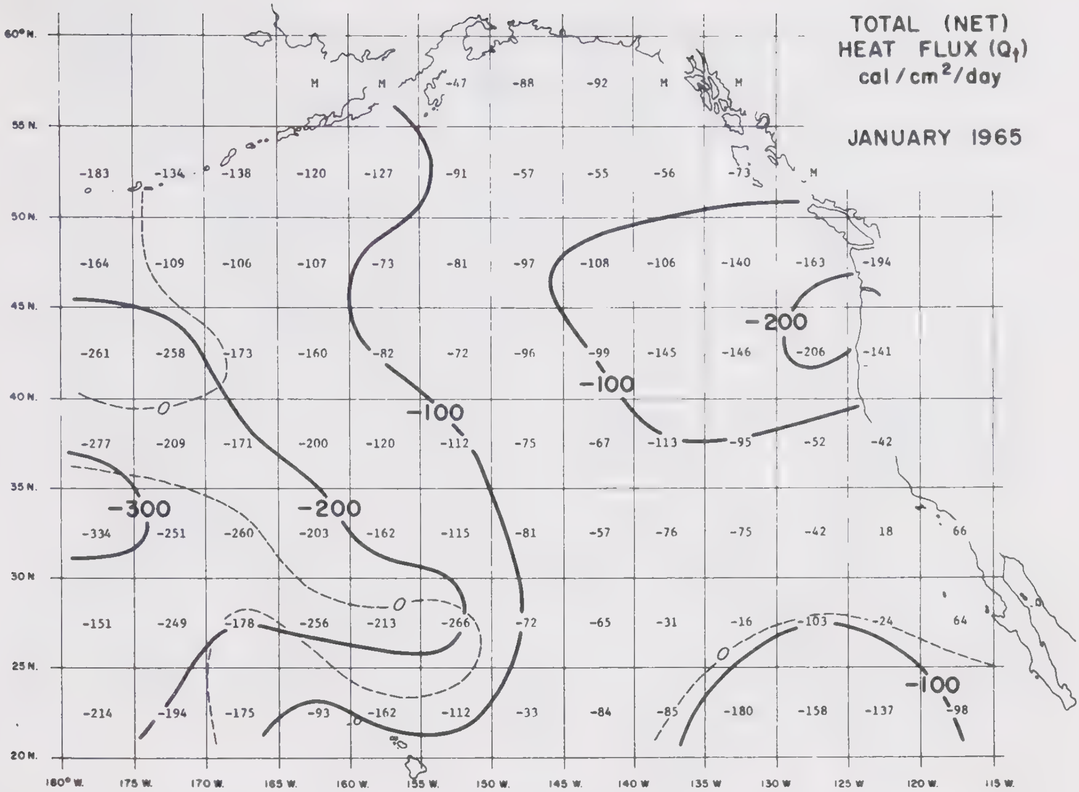
60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W
130 W.
125 W.
120 W.
115 W.
M 215 264 171 76 124 99
+100 +200 +100
157 138 113 110 111 122 143 97 122 61 146
0
136 139 156 148 158 172 117 121 95 118 101 144
0
206 240 218 218 170 193 191 138 136 121 176 311
+300 +200
122 32 252 250 223 167 143 89 128 116 149 312
+200 +100 +300 0 0
106 314 308 357 192 155 124 164 147 133 117 170 151
86 107 111 64 147 79 193 135 216 119 33 56 186
+100 +100 0
97 102 54 50 57 157 161 145 64 38 31 131 M


TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm^2 / day
SEPTEMBER 1964
M 15 114 -2 -31 40 M
44 68 4 49 57 54 31 50 50 63 114
29 19 8 30 20 57 77 104 106 82 99 126
-1 -71 -53 -55 -60 35 81 66 68 98 129 221
56 -20 16 78 38 45 46 63 39 26 129 207
101 100 149 164 121 129 0 1 1 -31 23 75 108
19 45 116 167 111 -60 -29 -48 7 -74 -38 18 130
-62 141 52 82 21 12 64 18 127 -11 -33 -103 62
0
+100
+200
-100
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm^2 / day
OCTOBER 1964
-17 -207 -136 -114 -156 -260 -84
-23 -88 -103 -85 -89 -147 -115 -81 -94 -20 M
4 -25 -55 -127 -115 -123 -83 -60 -31 -57 -36 -53
-167 -166 -211 -211 -178 -217 -165 -154 -92 -38 23 73
-130 -144 -256 -168 -248 -218 -181 -101 -28 51 64 107
12 -27 -139 -197 -131 -106 -106 -28 16 25 92 139 98
-198 -177 -218 -348 -305 -138 -84 -121 45 62 11 162 141
-49 -70 -158 -121 -135 -84 -42 78 60 15 105 103 90
-100
-200
-300
0
+100
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
NOVEMBER 1964
M M M -246 -286 -307 M
-146 -224 -209 -238 -215 -199 -192 -184 -216 -198 -172
-116 -136 -156 -161 -100 -140 -138 -183 -207 -236 -229 -226
-301 -209 -56 -259 -191 -114 -213 -242 -190 -189 -228 -130
-359 -232 -263 -209 -177 -199 -221 -206 -178 -159 -90 -38
-318 -328 -294 -202 -231 -162 -206 -186 -127 -127 -113 -6 10
-303 -395 -331 -210 -322 -249 -184 -205 -143 -89 -185 -50 36
-56 -17 -213 -147 -159 -170 -101 -112 -50 -143 -207 -237 -128
-200
-200
-200
0
0
-300
-200
-100
0
0
0
-200
-200
-100
-100
0
60° N.
55 N.
50 N.
45 N.
40 N
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W
165 W
160 W.
155 W
150 W.
145 W
140 W
135 W
130 W.
125 W.
120 W.
115 W.

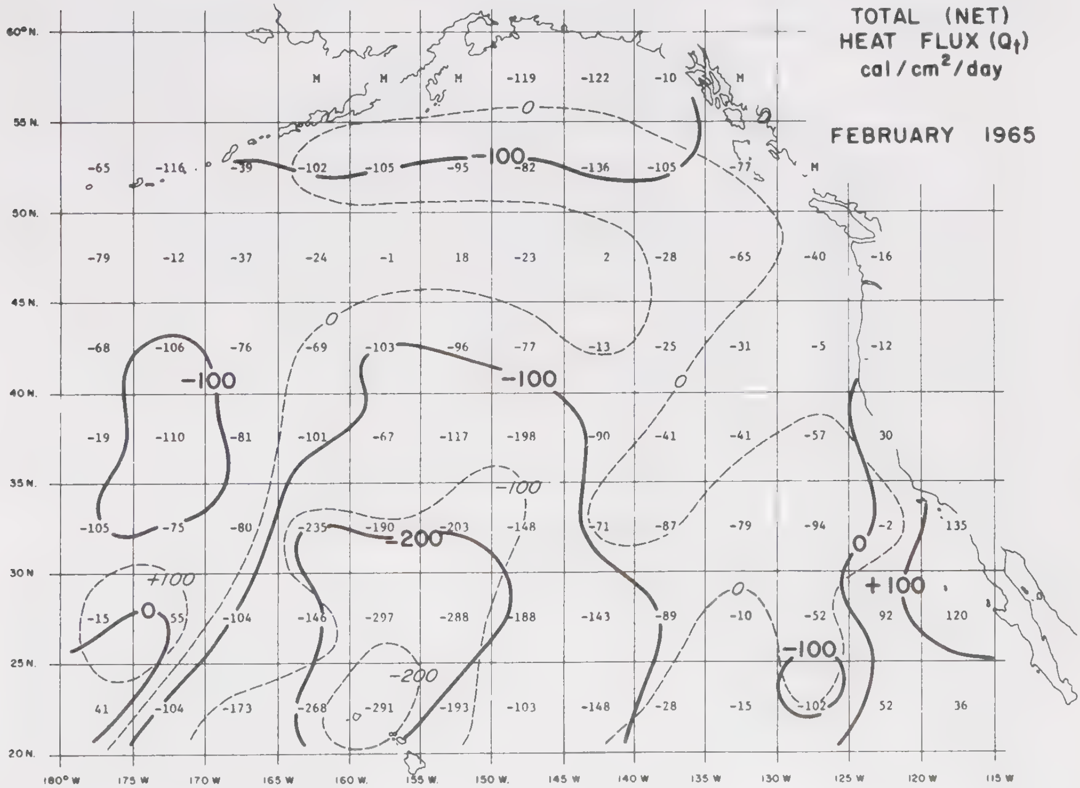

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
DECEMBER 1964
M M M -353 -320 -527 M
-100
-300
-58 -179 -177 -188 -148 -223 -208 -233 -252 -274 -385
0
-200
-96 -103 -163 -148 -178 -160 -167 -222 -233 -236 -193 -218
-100
-302 -321 -277 -358 -251 -250 -293 -268 -302 -275 -242 -159
-100
0
-368 -217 -222 -275 -264 -21 -192 -196 -150 -163 -94 -69
0
-200
-100
-300
+100
-325 -263 -299 -207 -137 -158 -65 -61 -93 -19 -44 -19 -49
+200
-625 -334 -290 -166 -47 -31 -54 -33 -8 2 -15 -45 -49
0
-100
-100
-475 -179 -278 -110 -55 -110 -43 -92 -71 -182 -165 -111 -9
+100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W
125 W.
120 W
115 W



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

JANUARY 1965

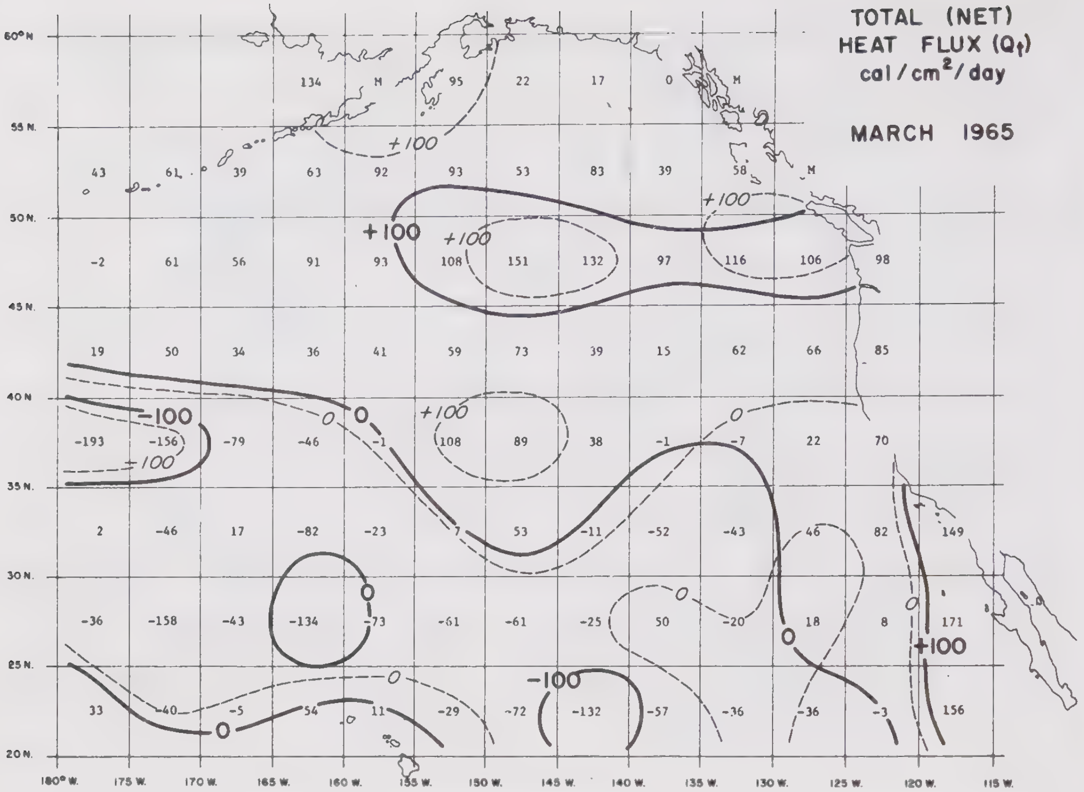
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W
135 W
130 W
125 W
120 W.
115 W.
M M -47 -88 -92 M M
-183 -134 -138 -120 -127 -91 -57 -55 -56 -73 M
-164 -109 -106 -107 -73 -81 -97 -108 -106 -140 -163 -194
-261 -258 -173 -160 -82 -72 -96 -99 -145 -146 -206 -141
-277 -209 -171 -200 -120 -112 -75 -67 -113 -95 -52 -42
-334 -251 -260 -203 -162 -115 -81 -57 -76 -75 -42 18 66
-151 -249 -178 -256 -213 -266 -72 -65 -31 -16 -103 -24 64
-214 -194 -175 -93 -162 -112 -33 -84 -85 -180 -158 -137 -98
0
-300
-200
-100
-100
-200
0
0
-100

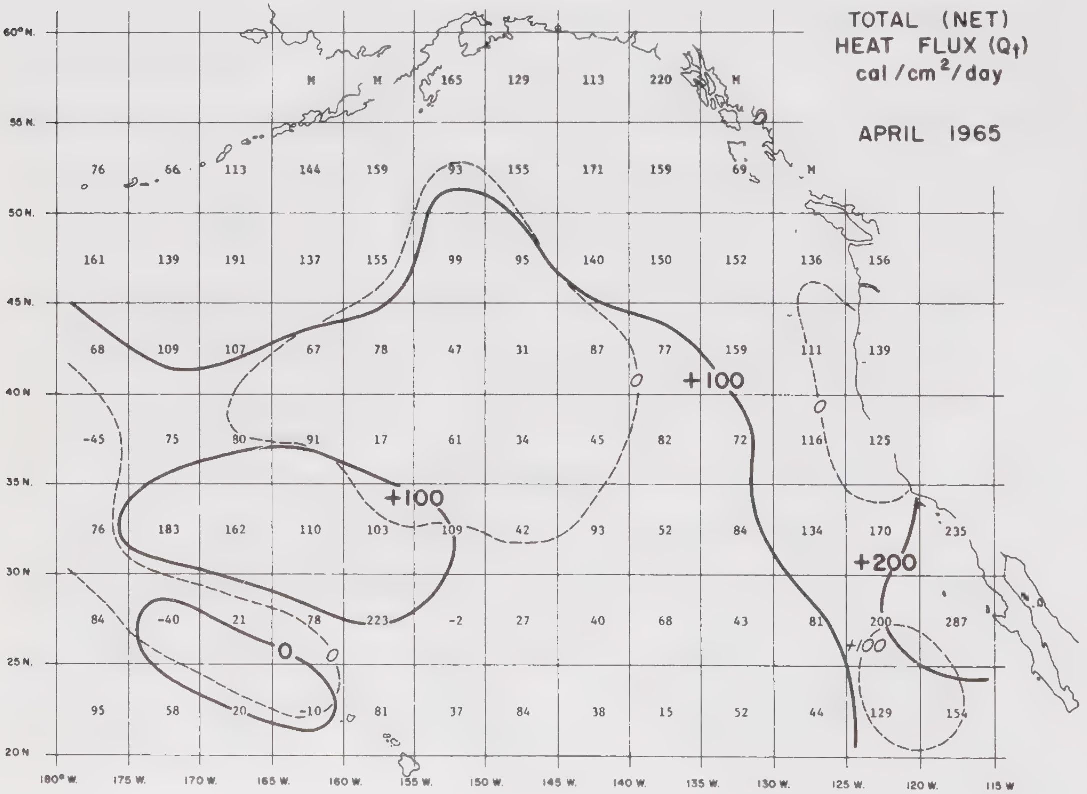


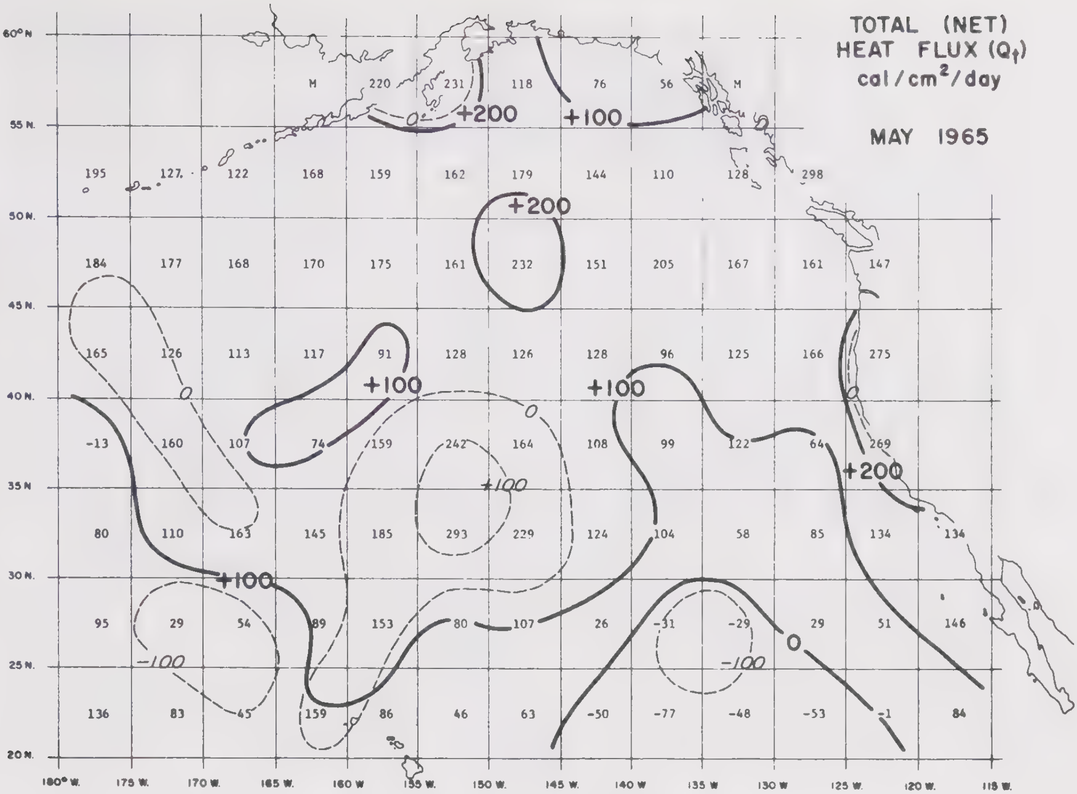
TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

FEBRUARY 1965

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W.
155 W.
150 W.
145 W
140 W
135 W
130 W
125 W
120 W
115 W
M M M -119 -122 -10 M
-65 -116 -39 -102 -105 -95 -82 -136 -105 -77 M
-79 -12 -37 -24 -1 18 -23 2 -28 -65 -40 -16
-68 -106 -76 -69 -103 -96 -77 -13 -25 -31 -5 -12
-19 -110 -81 -101 -67 -117 -198 -90 -41 -41 -57 30
-105 -75 -80 -235 -190 -203 -148 -71 -87 -79 -94 -2 135
-15 55 -104 -146 -297 -288 -188 -143 -89 -10 -52 92 120
41 -104 -173 -268 -291 -193 -103 -148 -28 -15 -102 52 36
-100
0
-100
-100
0
-100
-200
+100
0
-200
0
0
+100
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
MARCH 1965
60°N
55 N.
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
134 M 95 22 17 0 M
43 61 39 63 92 93 53 83 39 58 M
-2 61 56 91 93 108 151 132 97 116 106 98
19 50 34 36 41 59 73 39 15 62 66 85
-193 -156 -79 -46 -1 108 89 38 -1 -7 22 70
2 -46 17 -82 -23 7 53 -11 -52 -43 46 82 149
-36 -158 -43 -134 -73 -61 -61 -25 50 -20 18 8 171
33 -40 -5 54 11 -29 -72 -132 -57 -36 -36 -3 156
+100
+100
+100
+100
-100
-100
0
0
+100
0
0
0
0
+100
-100
0
0

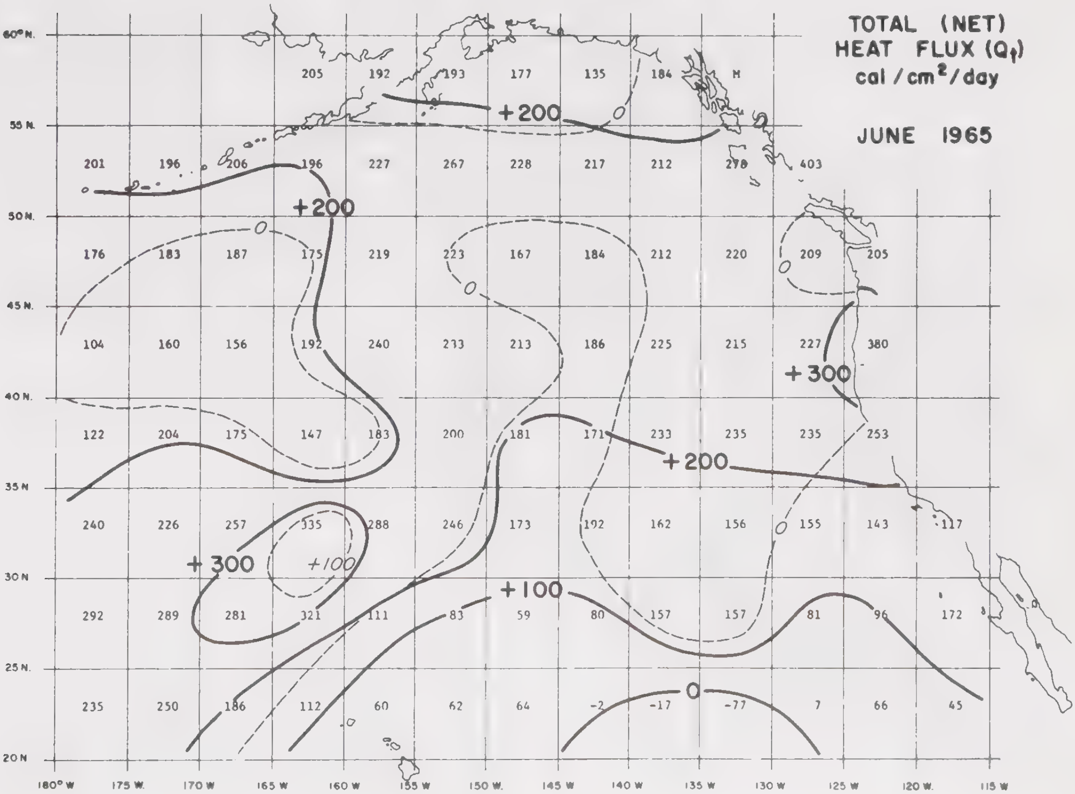

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
APRIL 1965
60°N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M M 165 129 113 220 M
76 66 113 144 159 93 155 171 159 69 M
161 139 191 137 155 99 95 140 150 152 136 156
68 109 107 67 78 47 31 87 77 159 111 139
-45 75 80 91 17 61 34 45 82 72 116 125
76 183 162 110 103 109 42 93 52 84 134 170 235
84 -40 21 78 223 -2 27 40 68 43 81 200 287
95 58 20 -10 81 37 84 38 15 52 44 129 154
0
+100
0
+100
0
0
0
+200
+100



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

MAY 1965

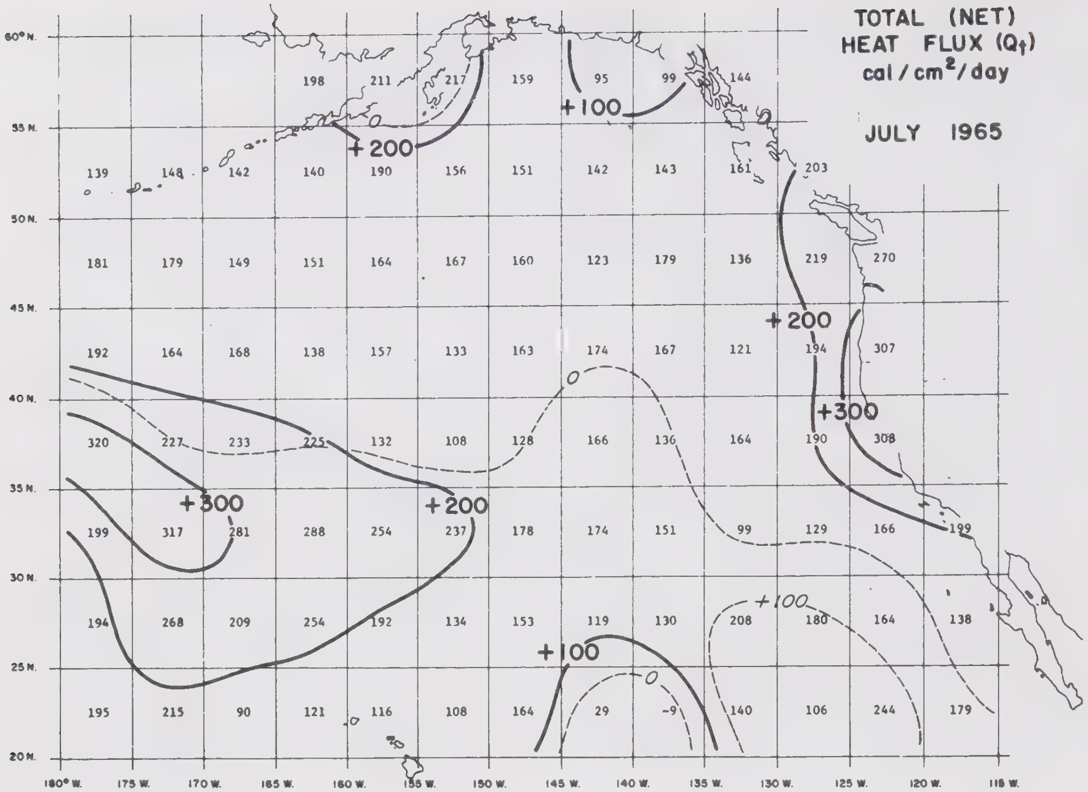
60° N
55 N.
50 N.
45 N.
40 N.
35 N
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W
155 W.
150 W.
145 W.
140 W
135 W
130 W
125 W.
120 W.
115 W.
M 220 231 118 76 56 M
+200
+100
0
195 127 122 168 159 162 179 144 110 128 298
+200
184 177 168 170 175 161 232 151 205 167 161 147
165 126 113 117 91 128 126 128 96 125 166 275
0
+100
+100
0
0
-13 160 107 74 159 242 164 108 99 122 64 269
+200
+100
80 110 163 145 185 293 229 124 104 58 85 134 134
+100
95 29 54 89 153 80 107 26 -31 -29 29 51 146
0
-100
-100
136 83 45 159 86 46 63 -50 -77 -48 -53 -1 84

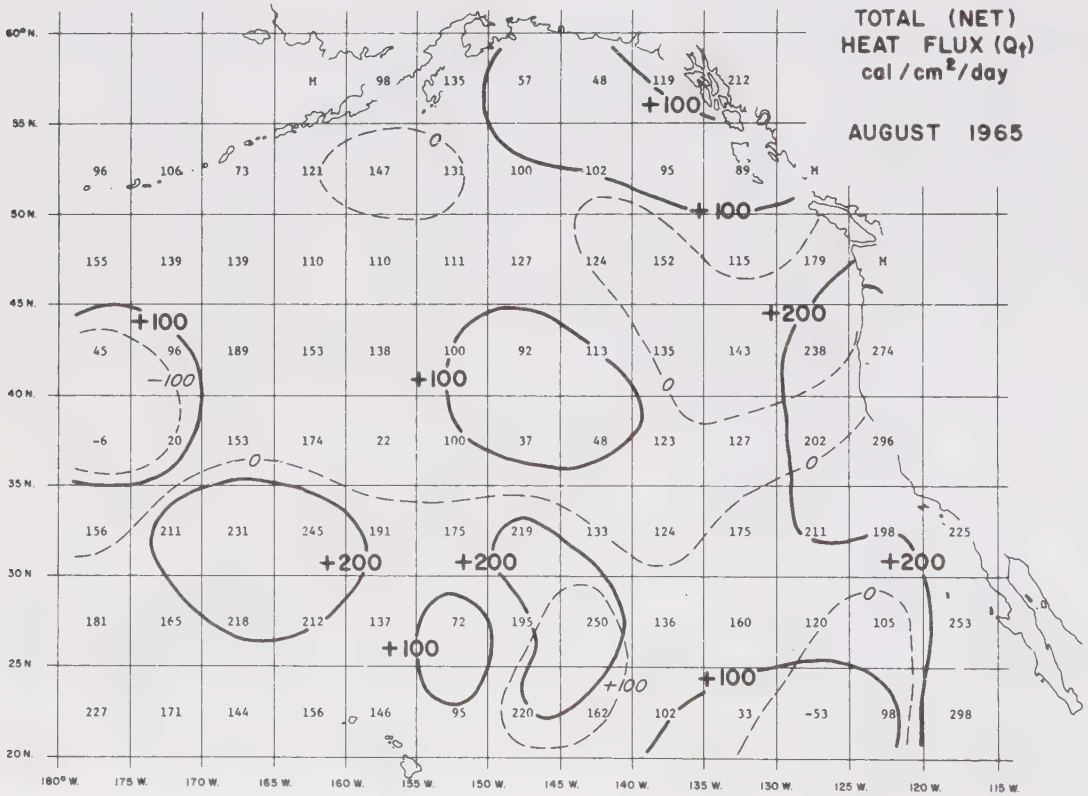


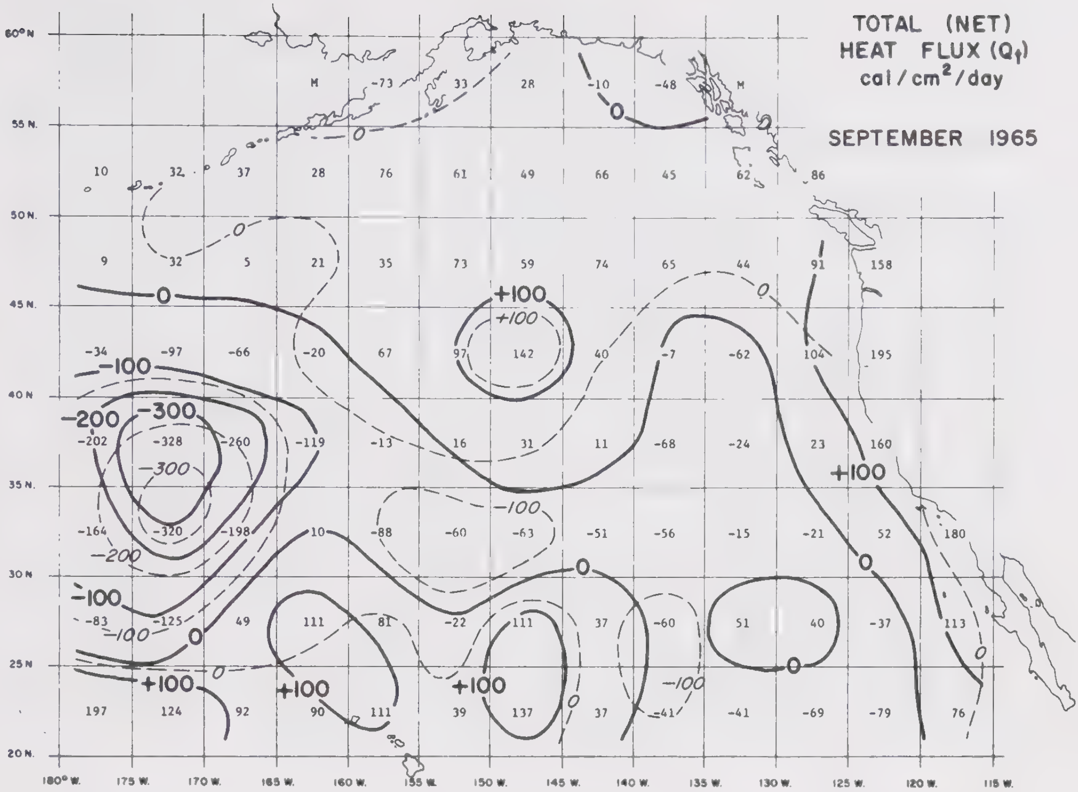
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JUNE 1965

60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N.
20 N
180° W
175 W.
170 W
165 W
160 W
155 W
150 W.
145 W
140 W
135 W
130 W
125 W
120 W.
115 W
205 192 193 177 135 184 M
+200
0
201 196 206 196 227 267 228 217 212 278 403
+200
0
176 183 187 175 219 223 167 184 212 220 209 205
0
0
104 160 156 192 240 233 213 186 225 215 227 380
+300
122 204 175 147 183 200 181 171 233 235 235 253
+200
240 226 257 335 288 246 173 192 162 156 155 143 117
0
+300
+100
292 289 281 321 111 83 59 80 157 157 81 96 172
+100
235 250 186 112 60 62 64 -2 -17 -77 7 66 45
0


TOTAL (NET) HEAT FLUX (Qt)
cal / cm² / day
JULY 1965
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
198 211 217 159 95 99 144
139 148 142 140 190 156 151 142 143 161 203
181 179 149 151 164 167 160 123 179 136 219 270
192 164 168 138 157 133 163 174 167 121 194 307
320 227 233 225 132 108 128 166 136 164 190 308
199 317 281 288 254 237 178 174 151 99 129 166 199
194 268 209 254 192 134 153 119 130 208 180 164 138
195 215 90 121 116 108 164 29 -9 140 106 244 179
+100
+200
0
+200
+300
+300
+200
0
+100
+100
0

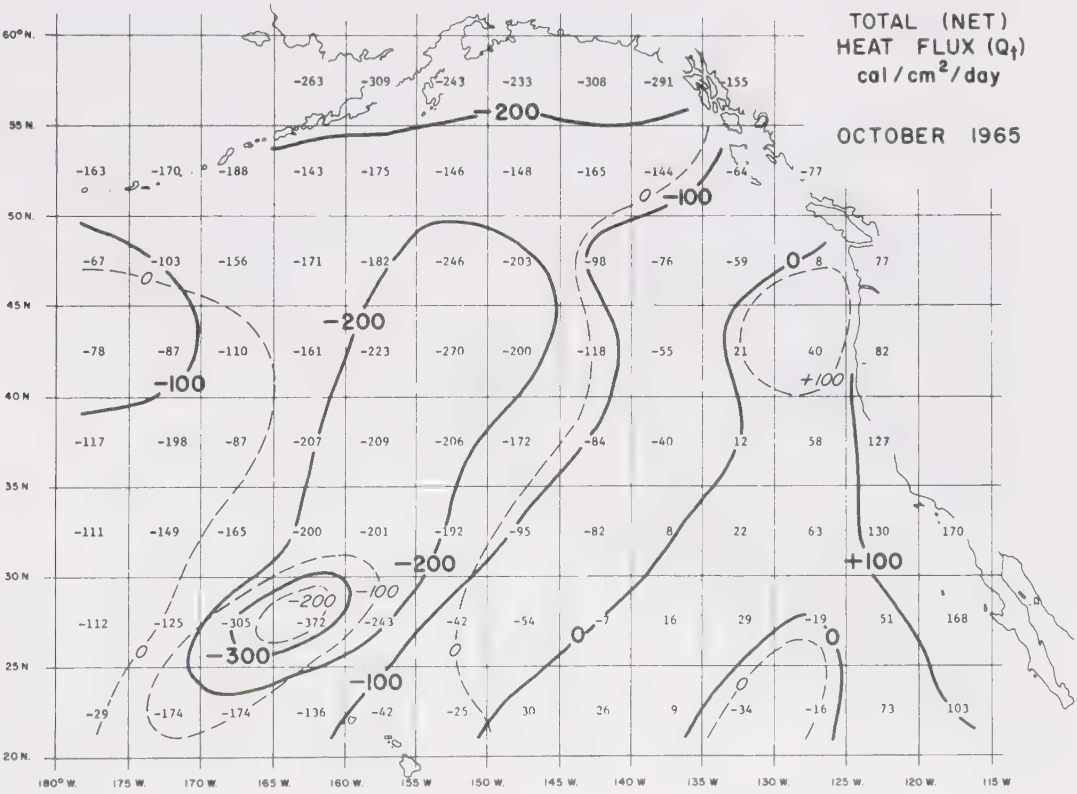

TOTAL (NET) HEAT FLUX (Qt)
cal / cm² / day
AUGUST 1965
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M 98 135 57 48 119 212
96 106 73 121 147 131 100 102 95 89 M
155 139 139 110 110 111 127 124 152 115 179 M
45 96 189 153 138 100 92 113 135 143 238 274
-6 20 153 174 22 100 37 48 123 127 202 296
156 211 231 245 191 175 219 133 124 175 211 198 225
181 165 218 212 137 72 195 250 136 160 120 105 253
227 171 144 156 146 95 220 162 102 33 -53 98 298
+100
0
+100
+100
-100
+100
+200
0
0
0
+200
+200
+200
+100
+100
+100
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

SEPTEMBER 1965

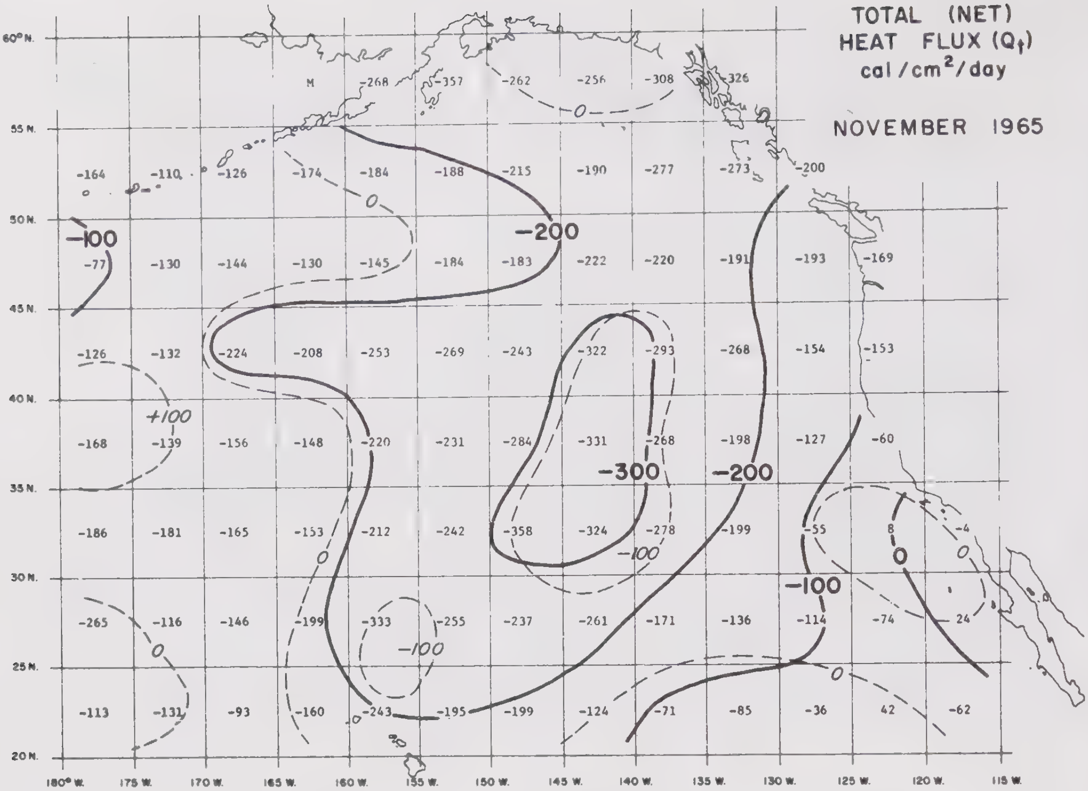
60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -73 33 28 -10 -48 M
10 32 37 28 76 61 49 66 45 62 86
9 32 5 21 35 73 59 74 65 44 91 158
-34 -97 -66 -20 67 97 142 40 -7 -62 104 195
-202 -328 -260 -119 -13 16 31 11 -68 -24 23 160
-164 -320 -198 10 -88 -60 -63 -51 -56 -15 -21 52 180
-83 -125 49 111 81 -22 111 37 -60 51 40 -37 113
197 124 92 90 111 39 137 37 -41 -41 -69 -79 76
0
+100
+100
-100
-200
-300
-300
-200
-100
-100
0
+100
+100
+100
0
0
0
-100
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

OCTOBER 1965

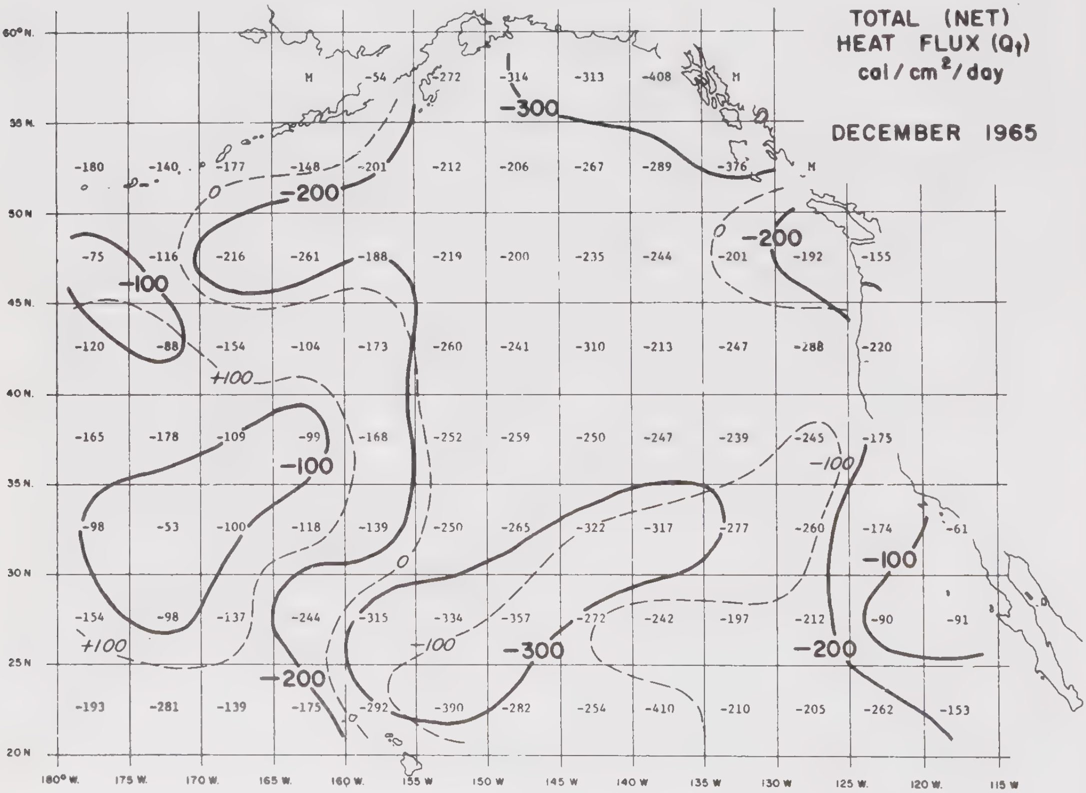
60° N.
55 N.
50 N.
45 N
40 N
35 N
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W.
145 W.
140 W
135 W
130 W.
125 W.
120 W.
115 W
-263 -309 -243 -233 -308 -291 -155
-163 -170 -188 -143 -175 -146 -148 -165 -144 -64 -77
-67 -103 -156 -171 -182 -246 -203 -98 -76 -59 8 77
-78 -87 -110 -161 -223 -270 -200 -118 -55 21 40 82
-117 -198 -87 -207 -209 -206 -172 -84 -40 12 58 127
-111 -149 -165 -200 -201 -192 -95 -82 8 22 63 130 170
-112 -125 -305 -372 -243 -42 -54 -7 16 29 -19 51 168
-29 -174 -174 -136 -42 -25 30 26 9 -34 -16 73 103
-200
0
-100
0
-200
-100
+100
-200
-100
-200
-300
-100
0
0
0
+100
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

NOVEMBER 1965

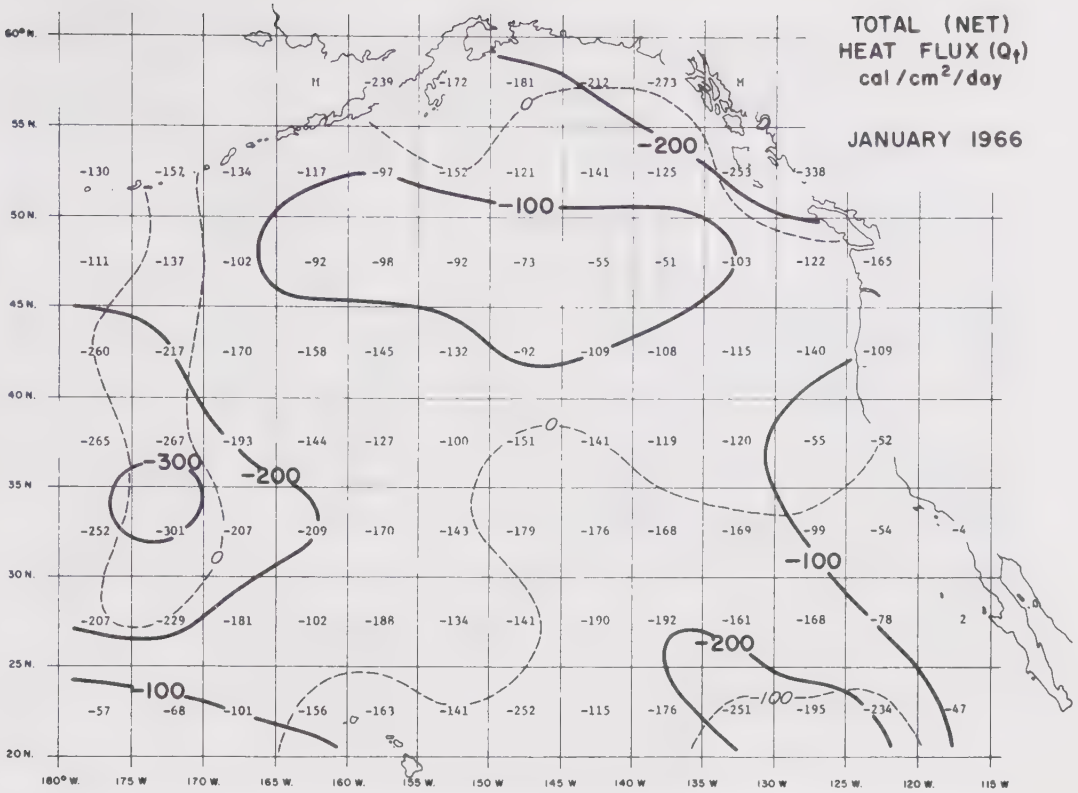
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -268 -357 -262 -256 -308 -326
-164 -110 -126 -174 -184 -188 -215 -190 -277 -273 -200
-77 -130 -144 -130 -145 -184 -183 -222 -220 -191 -193 -169
-126 -132 -224 -208 -253 -269 -243 -322 -293 -268 -154 -153
-168 -139 -156 -148 -220 -231 -284 -331 -268 -198 -127 -60
-186 -181 -165 -153 -212 -242 -358 -324 -278 -199 -55 8 -4
-265 -116 -146 -199 -333 -255 -237 -261 -171 -136 -114 -74 24
-113 -131 -93 -160 -243 -195 -199 -124 -71 -85 -36 42 -62
-100
-200
-300
+100
0
-100

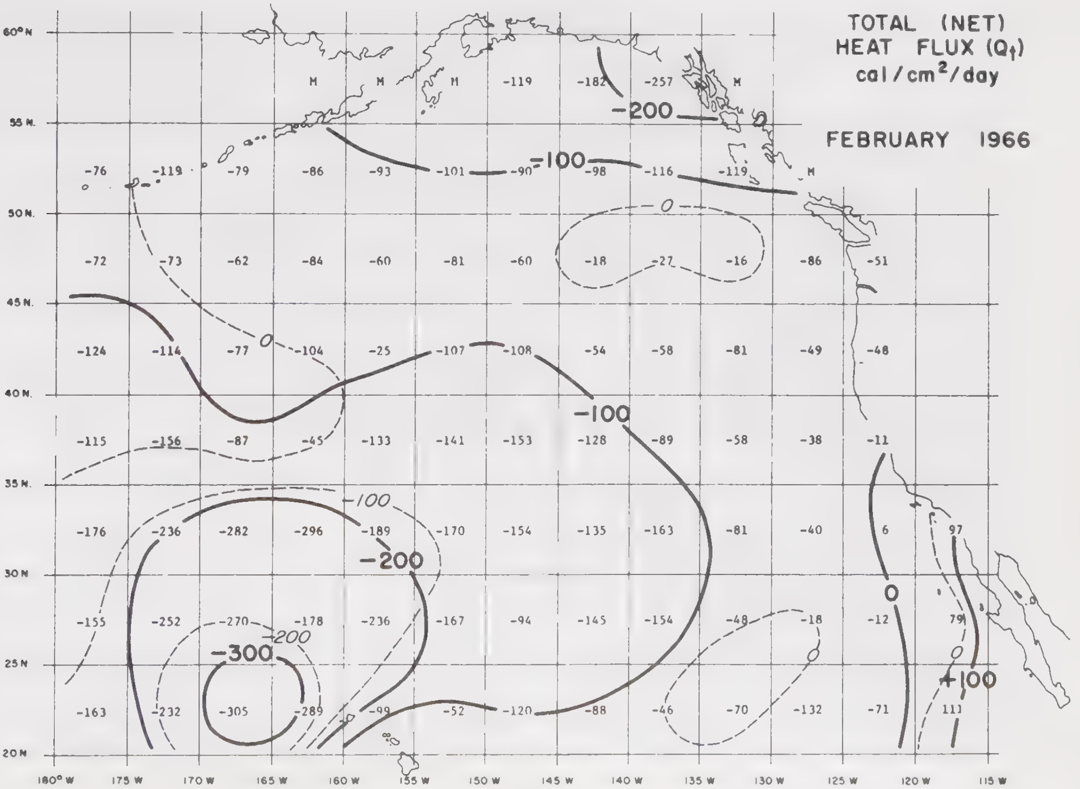


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

DECEMBER 1965

60° N.
55 N.
50 N
45 N.
40 N.
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W
145 W
140 W
135 W
130 W
125 W.
120 W.
115 W
M -54 -272 -314 -313 -408 M
-180 -140 -177 -148 -201 -212 -206 -267 -289 -376 M
-75 -116 -216 -261 -188 -219 -200 -235 -244 -201 -192 -155
-120 -88 -154 -104 -173 -260 -241 -310 -213 -247 -288 -220
-165 -178 -109 -99 -168 -252 -259 -250 -247 -239 -245 -175
-98 -53 -100 -118 -139 -250 -265 -322 -317 -277 -260 -174 -61
-154 -98 -137 -244 -315 -334 -357 -272 -242 -197 -212 -90 -91
-193 -281 -139 -175 -292 -390 -282 -254 -410 -210 -205 -262 -153
-300
-200
-100
+100
0
-100
-300
-200


TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
JANUARY 1966
60° N. 55 N. 50 N. 45 N. 40 N. 35 N 30 N. 25 N. 20 N.
180° W. 175 W 170 W. 165 W. 160 W. 155 W. 150 W 145 W 140 W 135 W 130 W 125 W. 120 W. 115 W
M -239 -172 -181 -212 -273 M
-130 -157 -134 -117 -97 -152 -121 -141 -125 -253 -338
-111 -137 -102 -92 -98 -92 -73 -55 -51 -103 -122 -165
-260 -217 -170 -158 -145 -132 -92 -109 -108 -115 -140 -109
-265 -267 -193 -144 -127 -100 -151 -141 -119 -120 -55 -52
-252 -301 -207 -209 -170 -143 -179 -176 -168 -169 -99 -54 -4
-207 -229 -181 -102 -188 -134 -141 -190 -192 -161 -168 -78 2
-57 -68 -101 -156 -163 -141 -252 -115 -176 -251 -195 -234 -47
-200
-100
-300
-200
-100
-200
-100
-100
0


TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day
FEBRUARY 1966
60° N 55 N. 50 N. 45 N. 40 N. 35 N. 30 N 25 N 20 N
180° W 175 W 170 W 165 W 160 W 155 W 150 W 145 W 140 W 135 W 130 W 125 W 120 W 115 W
M M M -119 -182 -257 M
-76 -119 -79 -86 -93 -101 -90 -98 -116 -119 M
-72 -73 -62 -84 -60 -81 -60 -18 -27 -16 -86 -51
-124 -114 -77 -104 -25 -107 -108 -54 -58 -81 -49 -48
-115 -156 -87 -45 -133 -141 -153 -128 -89 -58 -38 -11
-176 -236 -282 -296 -189 -170 -154 -135 -163 -81 -40 6 97
-155 -252 -270 -178 -236 -167 -94 -145 -154 -48 -18 -12 79
-163 -232 -305 -289 -99 -52 -120 -88 -46 -70 -132 -71 111
-200
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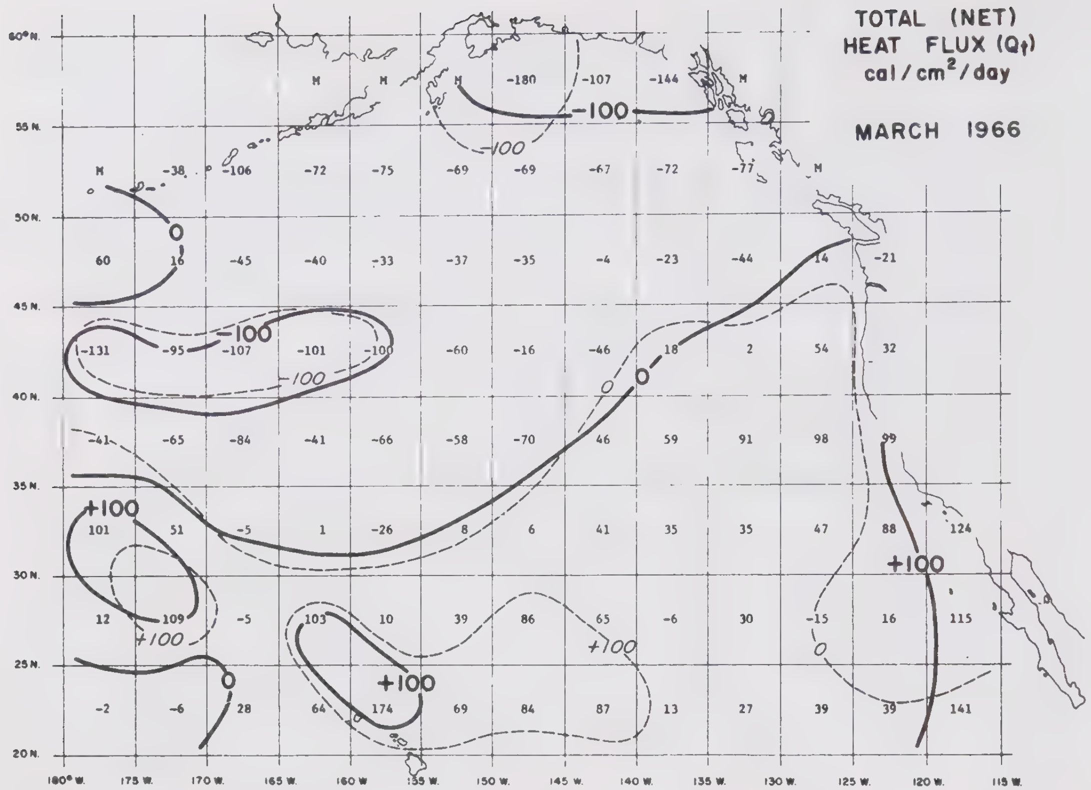
0
0
-100
-100
-200
-200
-300
0
0
+100


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
MARCH 1966
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M M -180 -107 -144 M
M -38 -106 -72 -75 -69 -69 -67 -72 -77 M
60 16 -45 -40 -33 -37 -35 -4 -23 -44 14 -21
-131 -95 -107 -101 -100 -60 -16 -46 18 2 54 32
-41 -65 -84 -41 -66 -58 -70 46 59 91 98 99
101 51 -5 1 -26 8 6 41 35 35 47 88 124
12 109 -5 103 10 39 86 65 -6 30 -15 16 115
-2 -6 28 64 174 69 84 87 13 27 39 39 141
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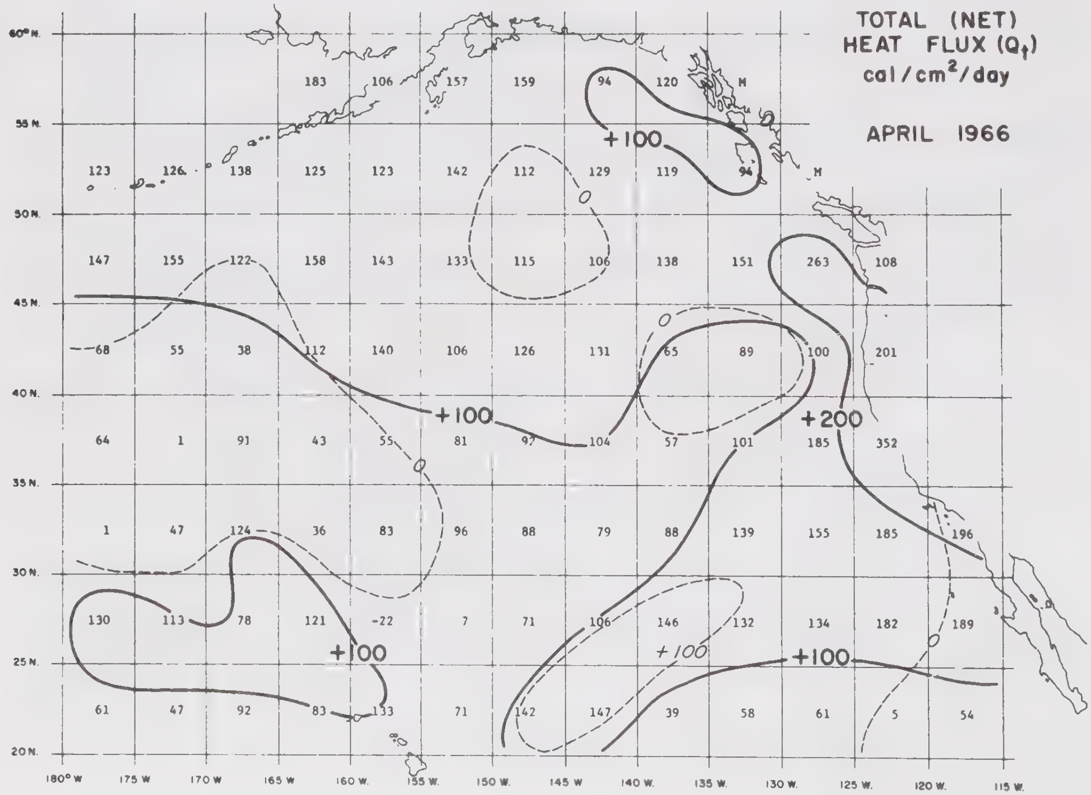
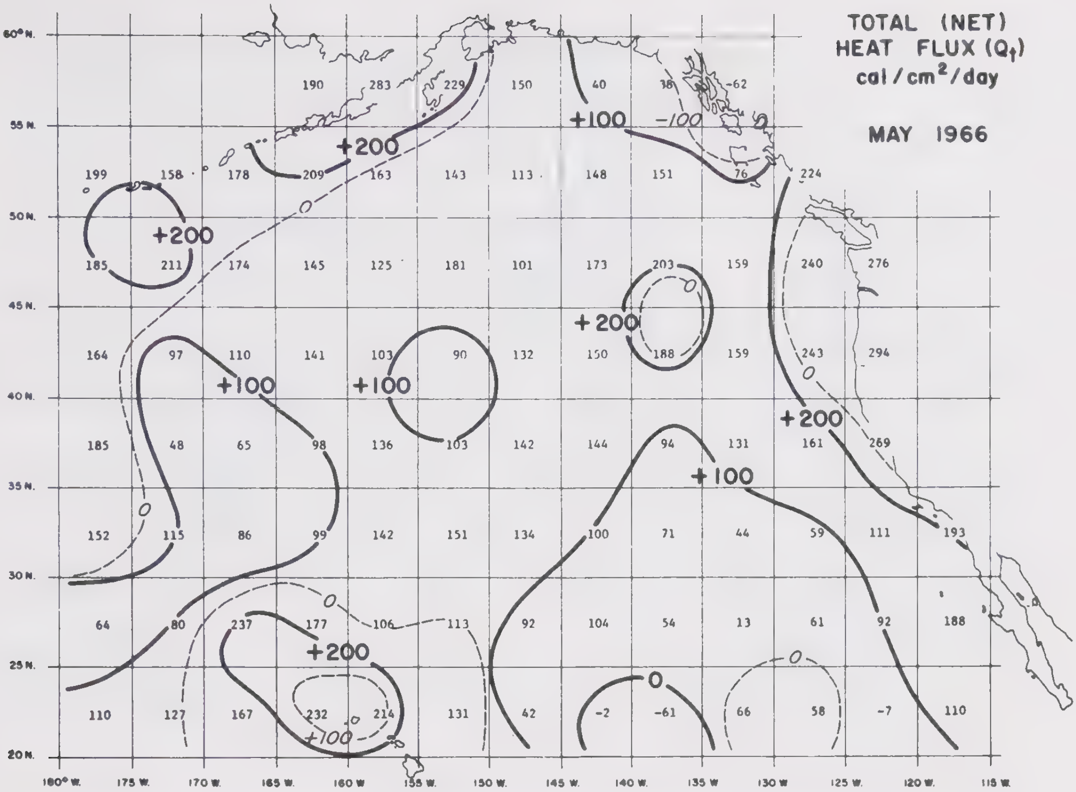
-100
-100
-100
0
0
0
0
0
+100
+100
+100
+100
+100


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
APRIL 1966
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W.
155 W.
150 W.
145 W
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
183 106 157 159 94 120 M
123 126 138 125 123 142 112 129 119 94 M
147 155 122 158 143 133 115 106 138 151 263 108
-68 55 38 112 140 106 126 131 65 89 100 201
64 1 91 43 55 81 97 104 57 101 185 352
1 47 124 36 83 96 88 79 88 139 155 185 196
130 113 78 121 -22 7 71 106 146 132 134 182 189
61 47 92 83 133 71 142 147 39 58 61 5 54
+100
+100
+200
+100
+100
+100
0
0
0
0


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
MAY 1966
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W
130 W
125 W.
120 W.
115 W.
190 283 229 150 40 38 -62
199 158 178 209 163 143 113 148 151 76 224
185 211 174 145 125 181 101 173 203 159 240 276
164 97 110 141 103 90 132 150 188 159 243 294
185 48 65 98 136 103 142 144 94 131 161 269
152 115 86 99 142 151 134 100 71 44 59 111 193
64 80 237 177 106 113 92 104 54 13 61 92 188
110 127 167 232 214 131 42 -2 -61 66 58 -7 110
+200
+100
-100
+200
0
+200
+200
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+100
+100
+200
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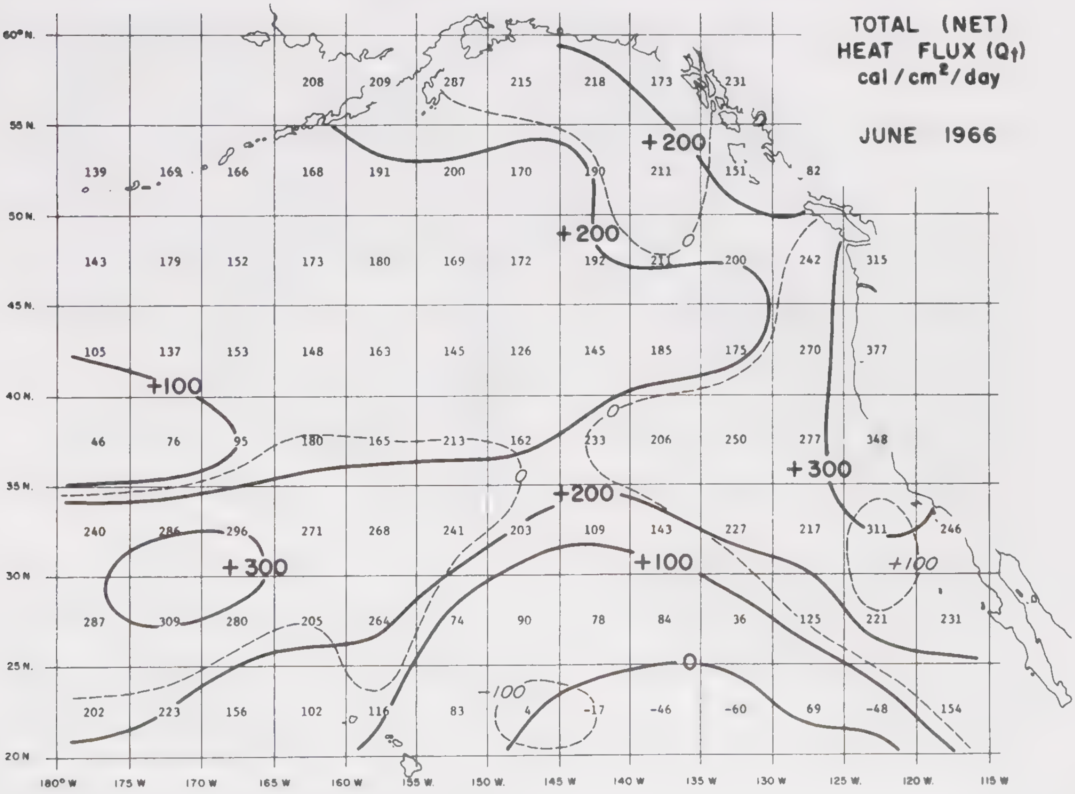
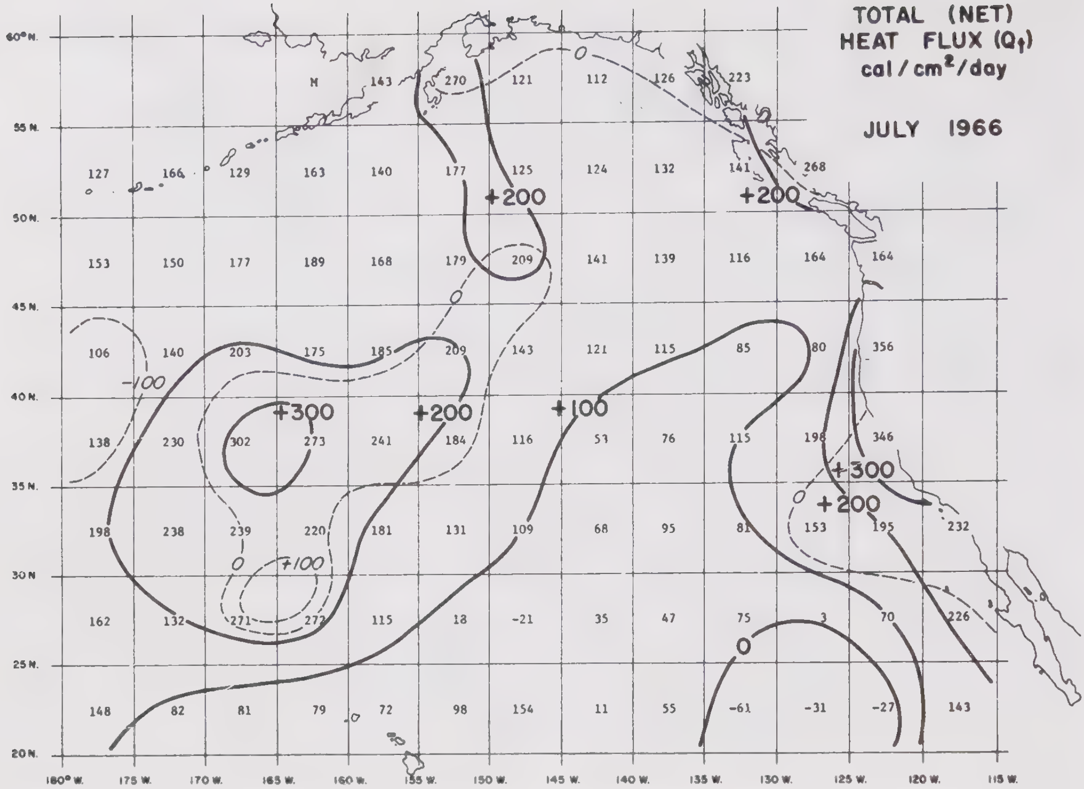
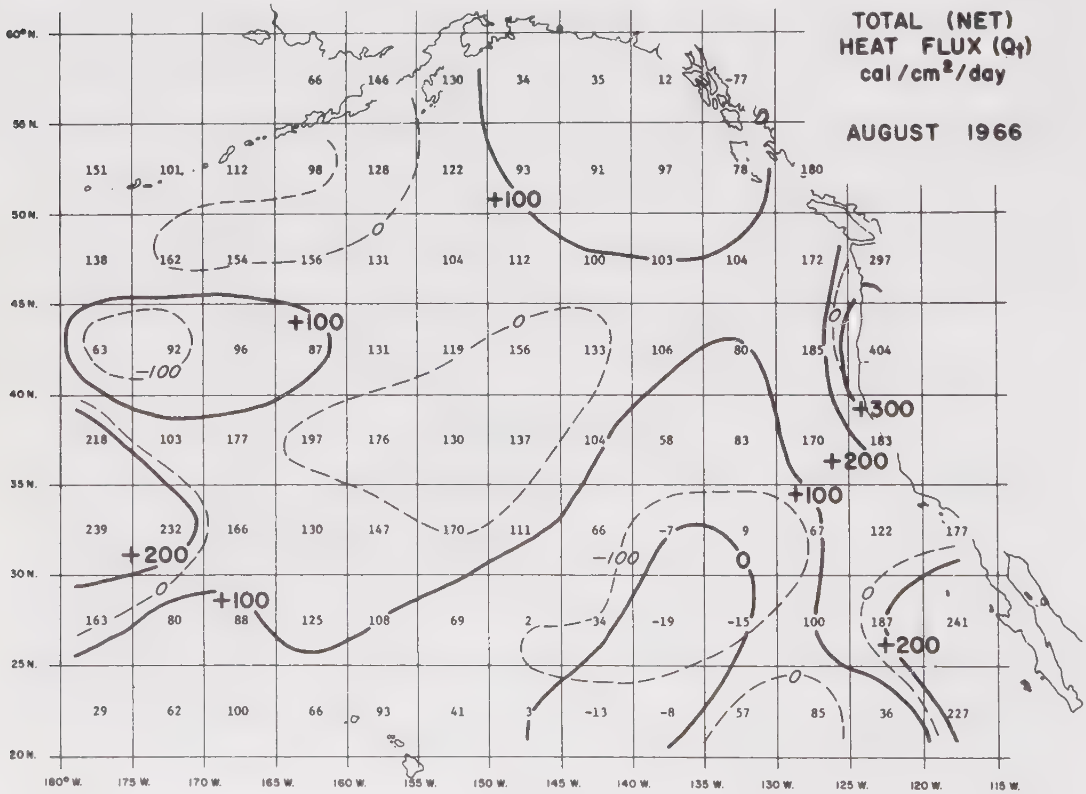
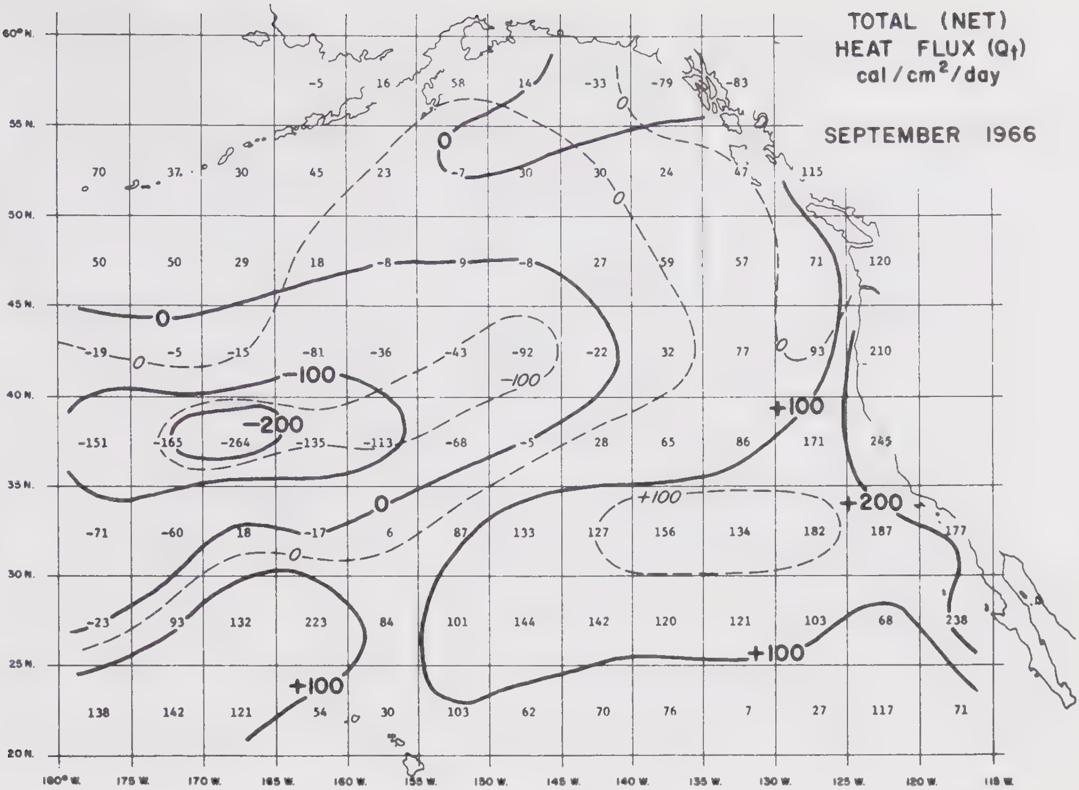
+100
0
+200
+100
0
0
0


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
JUNE 1966
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W
155 W.
150 W.
145 W
140 W
135 W
130 W
125 W.
120 W.
115 W
208 209 287 215 218 173 231
139 169 166 168 191 200 170 190 211 151 82
143 179 152 173 180 169 172 192 211 200 242 315
105 137 153 148 163 145 126 145 185 175 270 377
46 76 95 180 165 213 162 233 206 250 277 348
240 286 296 271 268 241 203 109 143 227 217 311 246
287 309 280 205 264 74 90 78 84 36 125 221 231
202 223 156 102 116 83 4 -17 -46 -60 69 -48 154
+200
+200
0
+100
0
+300
0
+200
+300
+100
+100
0
-100


TOTAL (NET)
HEAT FLUX (Q_T)
cal / cm² / day
JULY 1966
+300
+200
+100
0
-100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

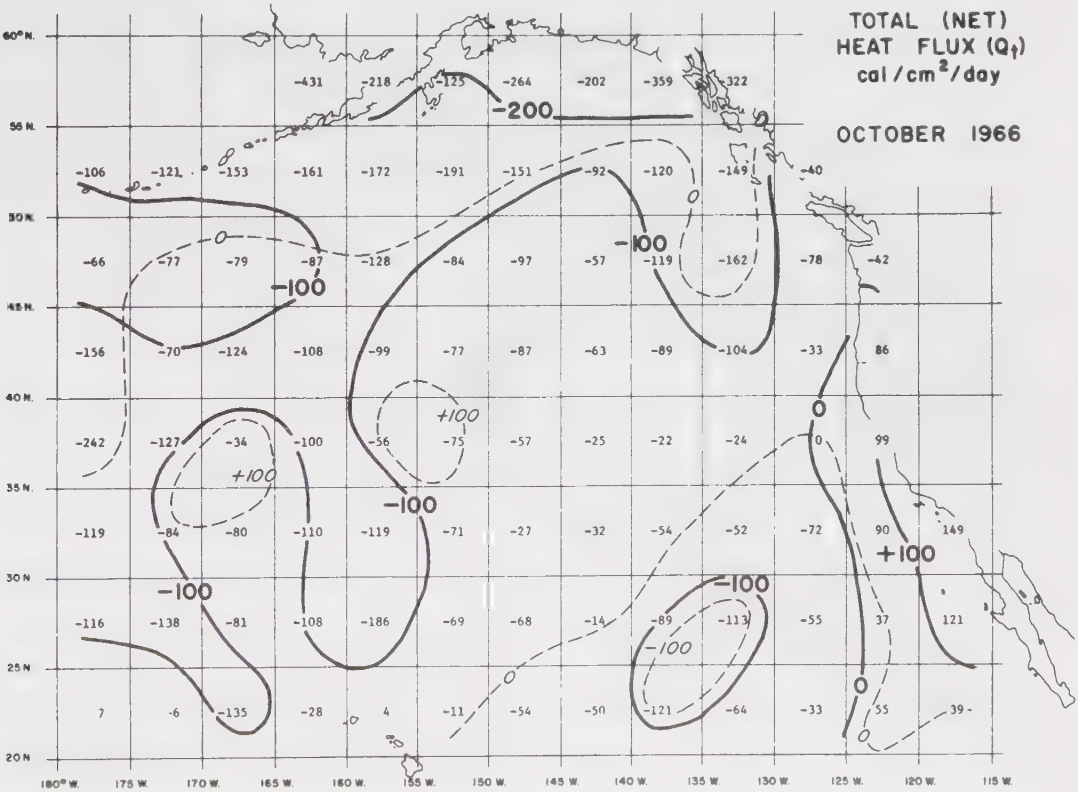

TOTAL (NET)
HEAT FLUX (Q_T)
cal / cm² / day
AUGUST 1966
+300
+200
+100
0
-100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

SEPTEMBER 1966

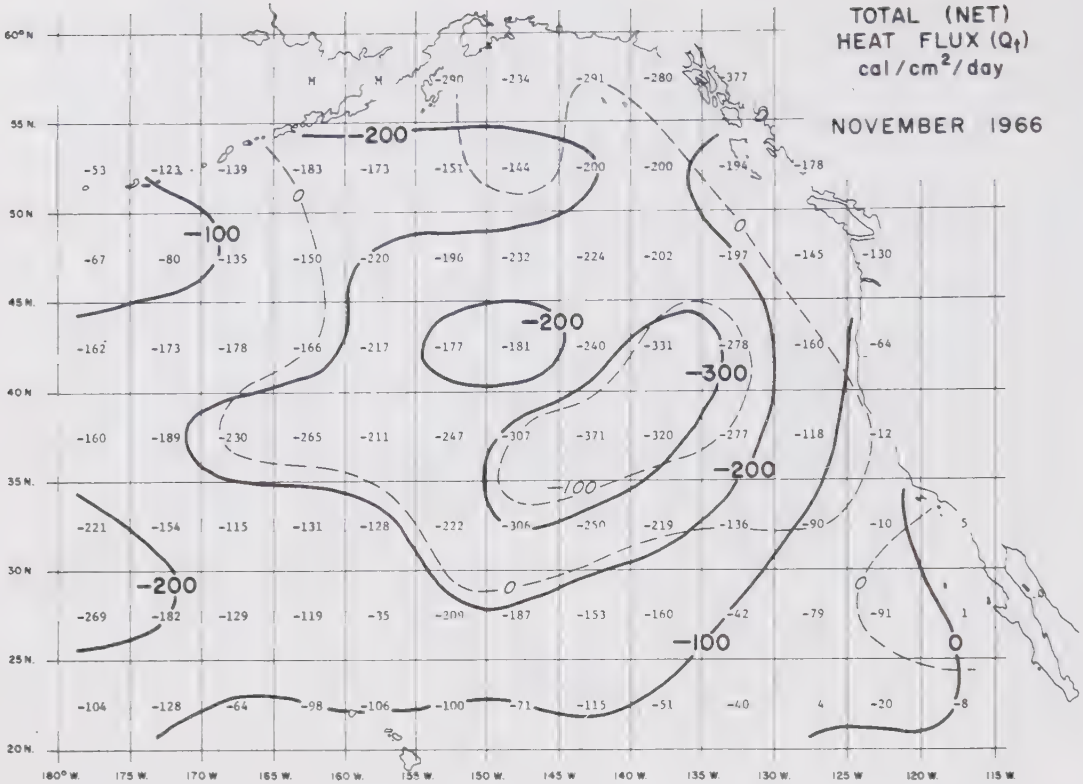
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-5 16 58 14 -33 -79 -83
70 37 30 45 23 -7 30 30 24 47 115
50 50 29 18 -8 9 -8 27 59 57 71 120
-19 -5 -15 -81 -36 -43 -92 -22 32 77 93 210
-151 -165 -264 -135 -113 -68 -5 28 65 86 171 245
-71 -60 18 -17 6 87 133 127 156 134 182 187 177
-23 93 132 223 84 101 144 142 120 121 103 68 238
138 142 121 54 30 103 62 70 76 7 27 117 71
0
-100
-200
+100
+200
-100
+100

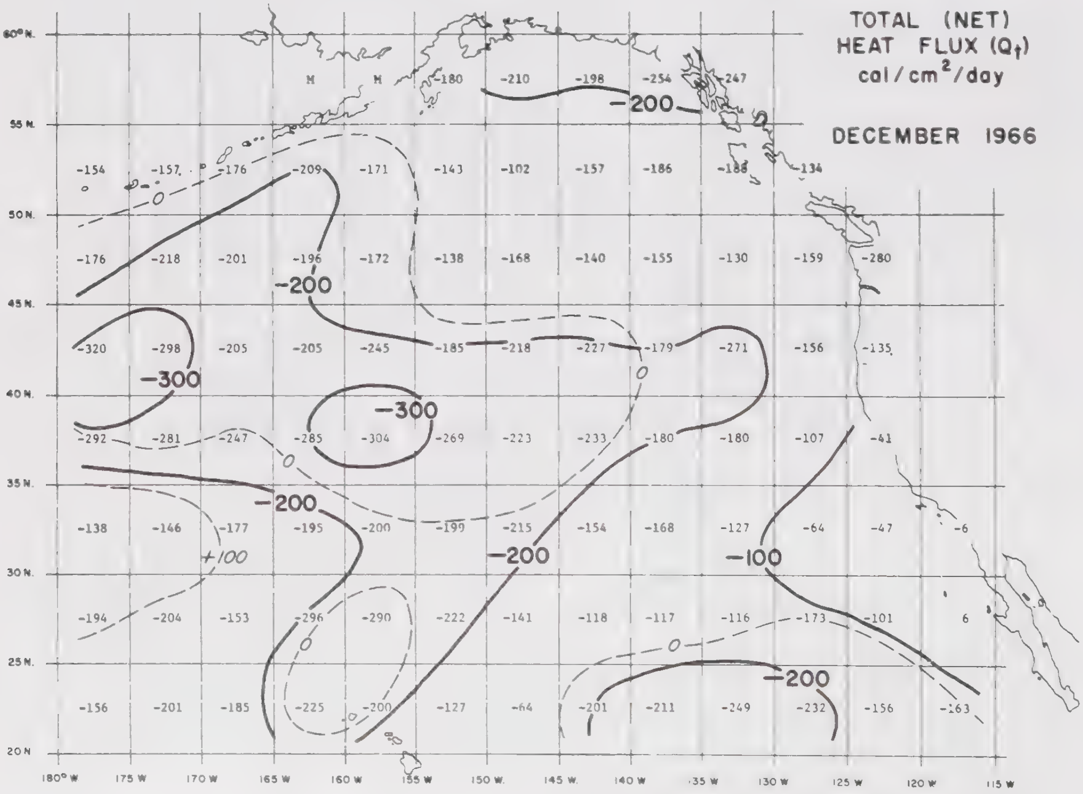


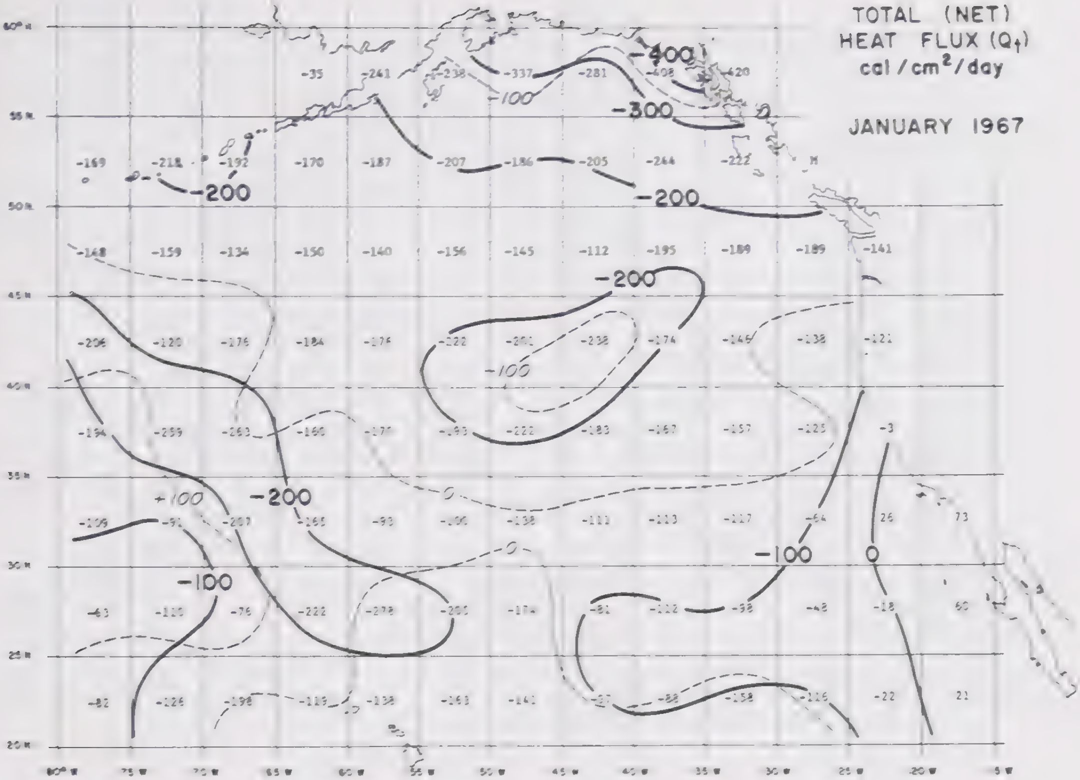
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

OCTOBER 1966

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-431 -218 -125 -264 -202 -359 -322
-106 -121 -153 -161 -172 -191 -151 -92 -120 -149 -40
-66 -77 -79 -87 -128 -84 -97 -57 -119 -162 -78 -42
-156 -70 -124 -108 -99 -77 -87 -63 -89 -104 -33 86
-242 -127 -34 -100 -56 -75 -57 -25 -22 -24 0 99
-119 -84 -80 -110 -119 -71 -27 -32 -54 -52 -72 90 149
-116 -138 -81 -108 -186 -69 -68 -14 -89 -113 -55 37 121
7 -6 -135 -28 4 -11 -54 -50 -121 -64 -33 55 39
-200
-100
0
+100


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
NOVEMBER 1966
60° N
55 N.
50 N
45 N.
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W
165 W.
160 W.
155 W.
150 W.
145 W
140 W.
135 W.
130 W.
125 W
120 W.
115 W
M
M
-290
-234
-291
-280
-377
-53
-123
-139
-183
-173
-151
-144
-200
-200
-194
-178
-67
-80
-135
-150
-220
-196
-232
-224
-202
-197
-145
-130
-162
-173
-178
-166
-217
-177
-181
-240
-331
-278
-160
-64
-160
-189
-230
-265
-211
-247
-307
-371
-320
-277
-118
-12
-221
-154
-115
-131
-128
-222
-306
-250
-219
-136
-90
-10
5
-269
-182
-129
-119
-35
-209
-187
-153
-160
-42
-79
-91
1
-104
-128
-64
-98
-106
-100
-71
-115
-51
-40
4
-20
-8
-200
-100
-200
-300
-200
-100
-200
-100
0
0
0
0

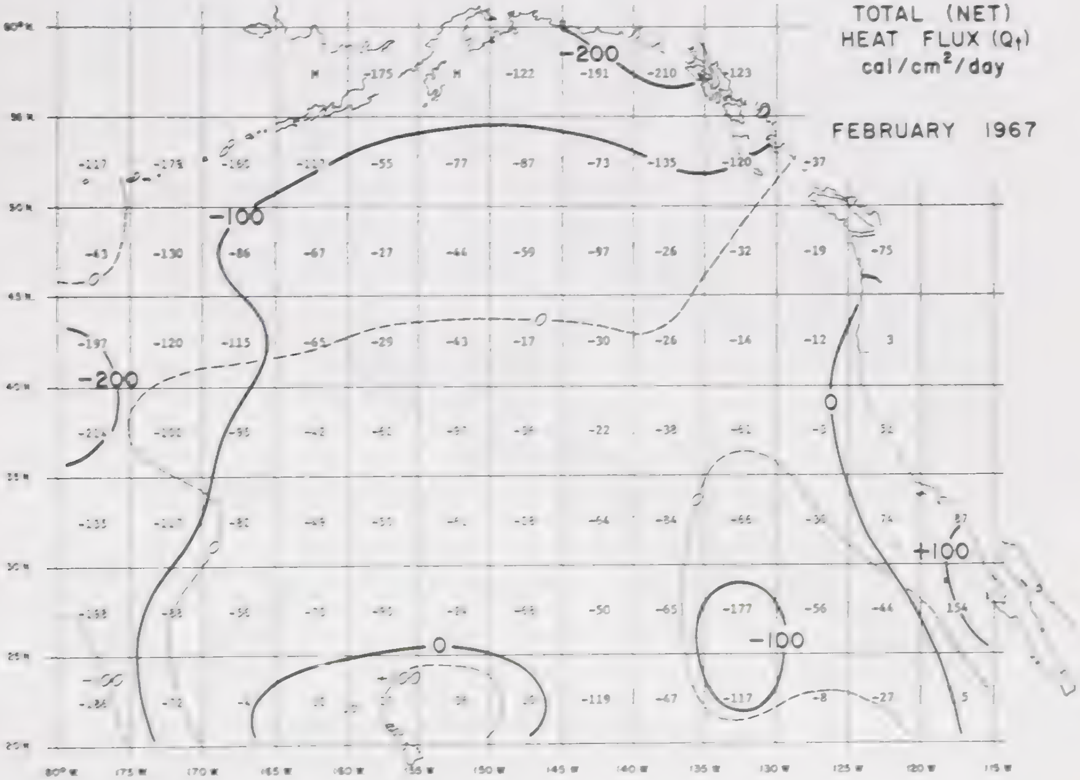

TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
DECEMBER 1966
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W.
145 W.
140 W
135 W
130 W
125 W
120 W
115 W
M
M
-180
-210
-198
-254
-247
-154
-157
-176
-209
-171
-143
-102
-157
-186
-188
-134
-176
-218
-201
-196
-172
-138
-168
-140
-155
-130
-159
-280
-320
-298
-205
-205
-245
-185
-218
-227
-179
-271
-156
-135
-292
-281
-247
-285
-304
-269
-223
-233
-180
-180
-107
-41
-138
-146
-177
-195
-200
-199
-215
-154
-168
-127
-64
-47
-6
-194
-204
-153
-296
-290
-222
-141
-118
-117
-116
-173
-101
6
-156
-201
-185
-225
-200
-127
-64
-201
-211
-249
-232
-156
-163
-200
-200
-300
-300
-200
-200
-100
-200
+100
0
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JANUARY 1967

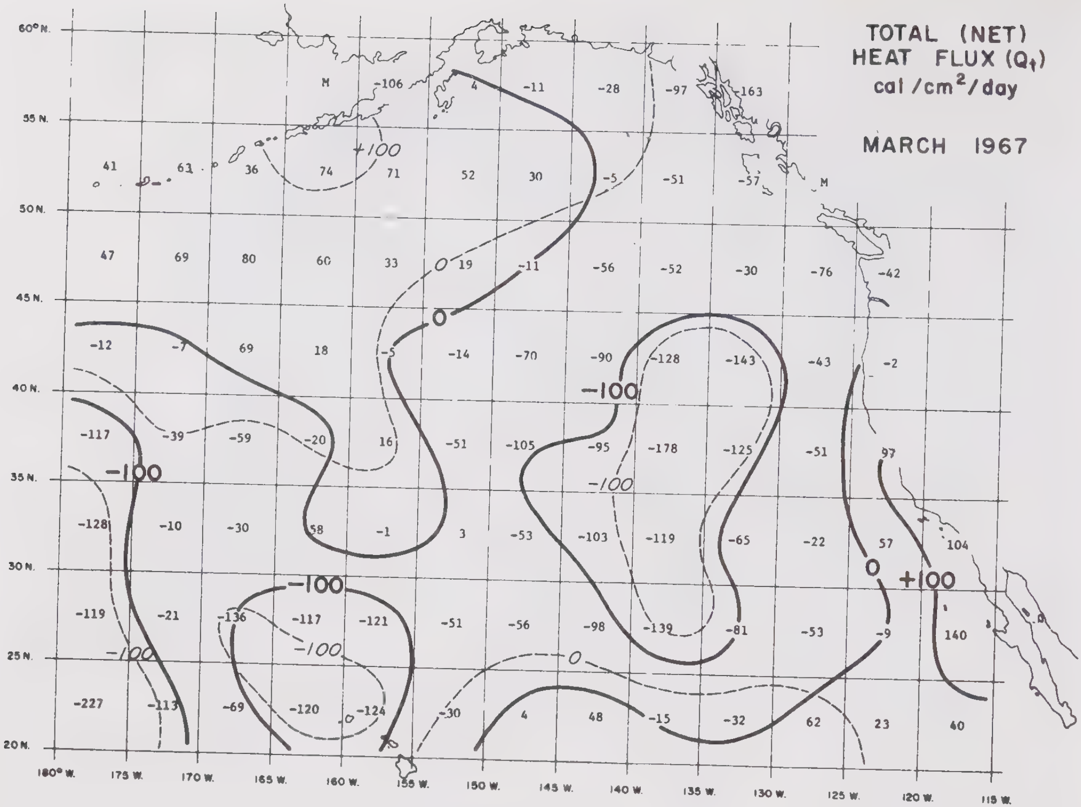
60° N
55 N
50 N
45 N
40 N
35 N
30 N
25 N
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W
120 W
115 W
-400
-300
-200
-100
0
+100
-35 -241 -238 -337 -281 -408 -420
-169 -218 -192 -170 -187 -207 -186 -205 -244 -222 M
-168 -159 -134 -150 -140 -156 -145 -112 -195 -189 -189 -141
-206 -120 -176 -184 -176 -122 -201 -238 -174 -146 -138 -121
-194 -259 -263 -160 -177 -193 -222 -183 -167 -157 -125 -3
-109 -91 -207 -165 -93 -106 -138 -111 -113 -117 -64 26 73
-63 -120 -76 -222 -278 -200 -174 -81 -112 -98 -48 -18 60
-82 -126 -198 -123 -138 -163 -141 -37 -88 -158 -116 -22 21



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

FEBRUARY 1967

60° N
55 N
50 N
45 N
40 N
35 N
30 N
25 N
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W
120 W
115 W
-200
-100
0
+100
M -175 M -122 -191 -210 -123
-217 -178 -160 -112 -55 -77 -87 -73 -135 -120 -37
-43 -130 -86 -67 -27 -66 -59 -97 -26 -32 -19 -75
-197 -120 -115 -65 -29 -63 -17 -30 -26 -14 -12 3
-214 -100 -95 -42 -61 -57 -36 -22 -38 -61 -5 32
-135 -117 -80 -49 -51 -41 -38 -64 -84 -66 -30 74 87
-138 -83 -56 -73 -90 -24 -48 -50 -65 -177 -56 -44 154
-186 -72 -4 -119 -67 -117 -8 -27 5



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

MARCH 1967

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
-106
4
-11
-28
-97
-163
41
61
36
74
+100
71
52
30
-5
-51
-57
M
47
69
80
60
33
0
19
-11
-56
-52
-30
-76
-42
0
-12
-7
69
18
-5
-14
-70
-90
-128
-143
-43
-2
-100
-117
-39
-59
-20
16
-51
-105
-95
-178
-125
-51
97
-100
-100
-128
-10
-30
58
-1
3
-53
-103
-119
-65
-22
57
104
0
+100
-100
-119
-21
-136
-117
-121
-51
-56
-98
-139
-81
-53
-9
140
-100
0
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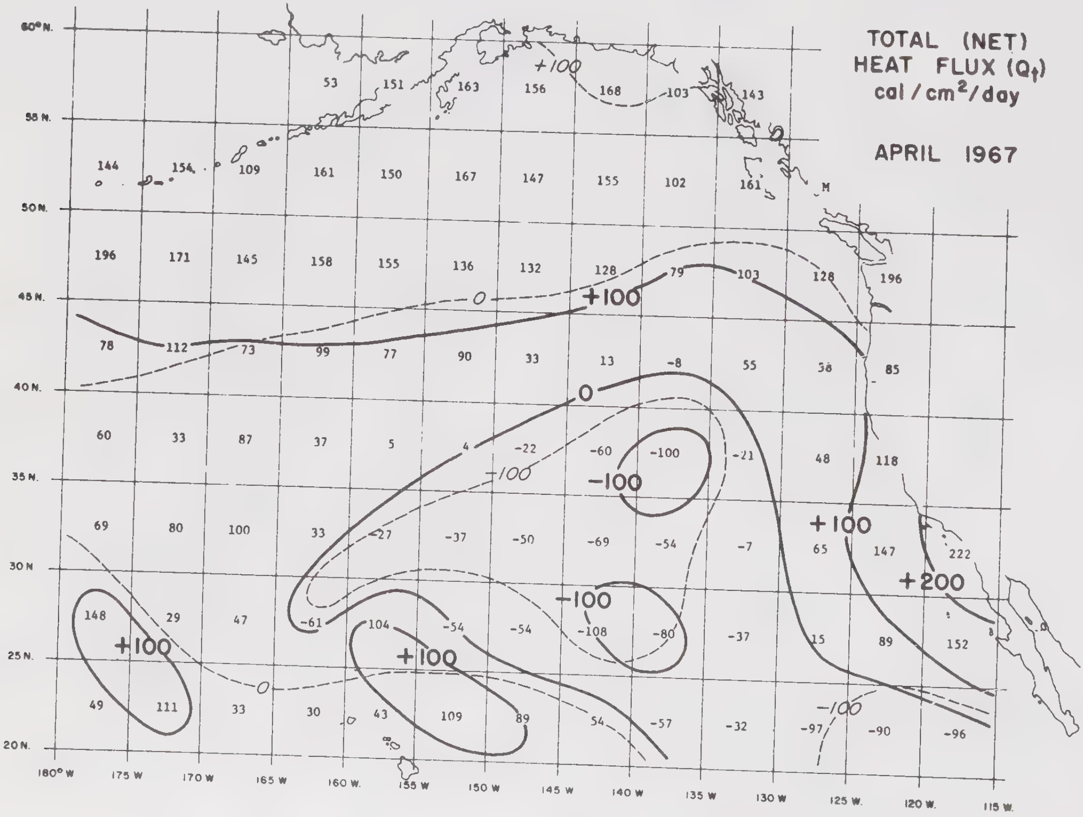
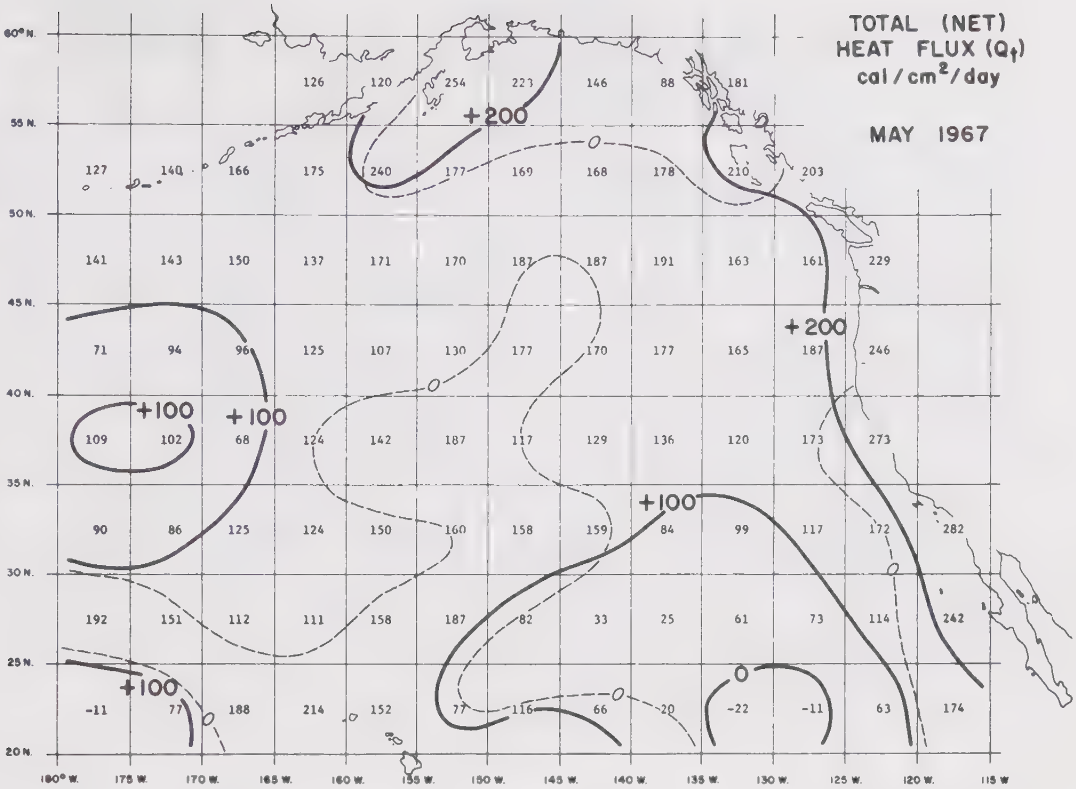
-113
-69
-120
-124
-30
4
48
-15
-32
62
23
40

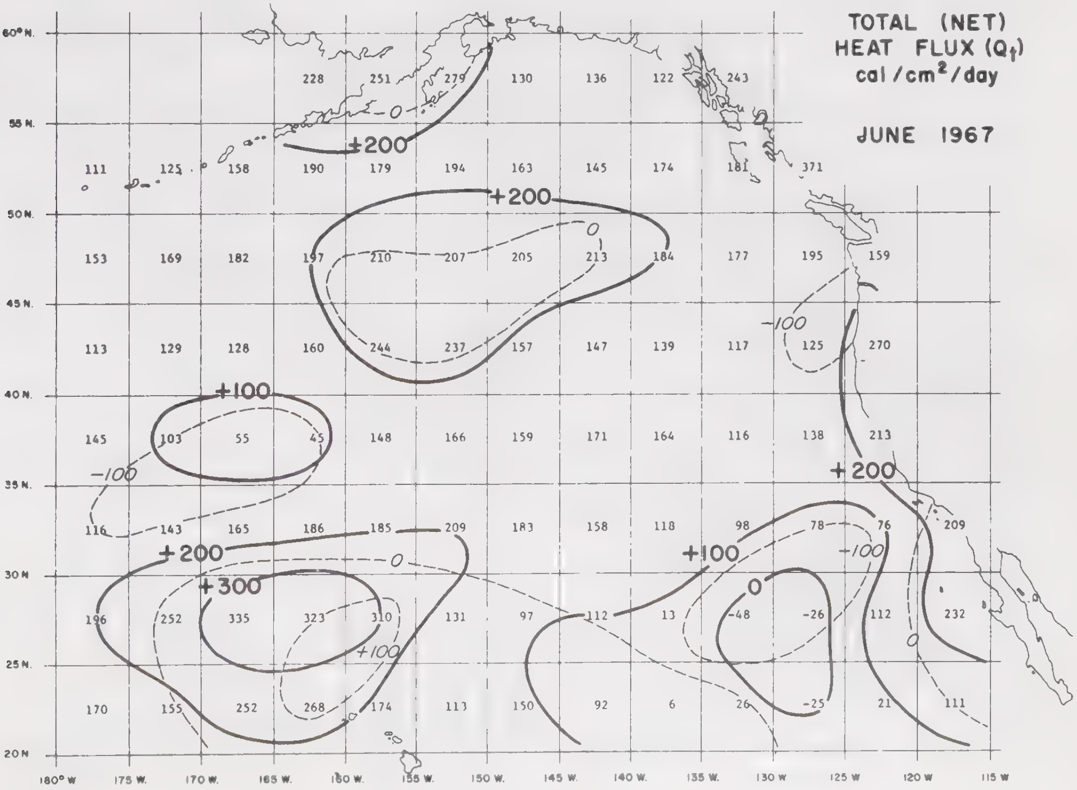


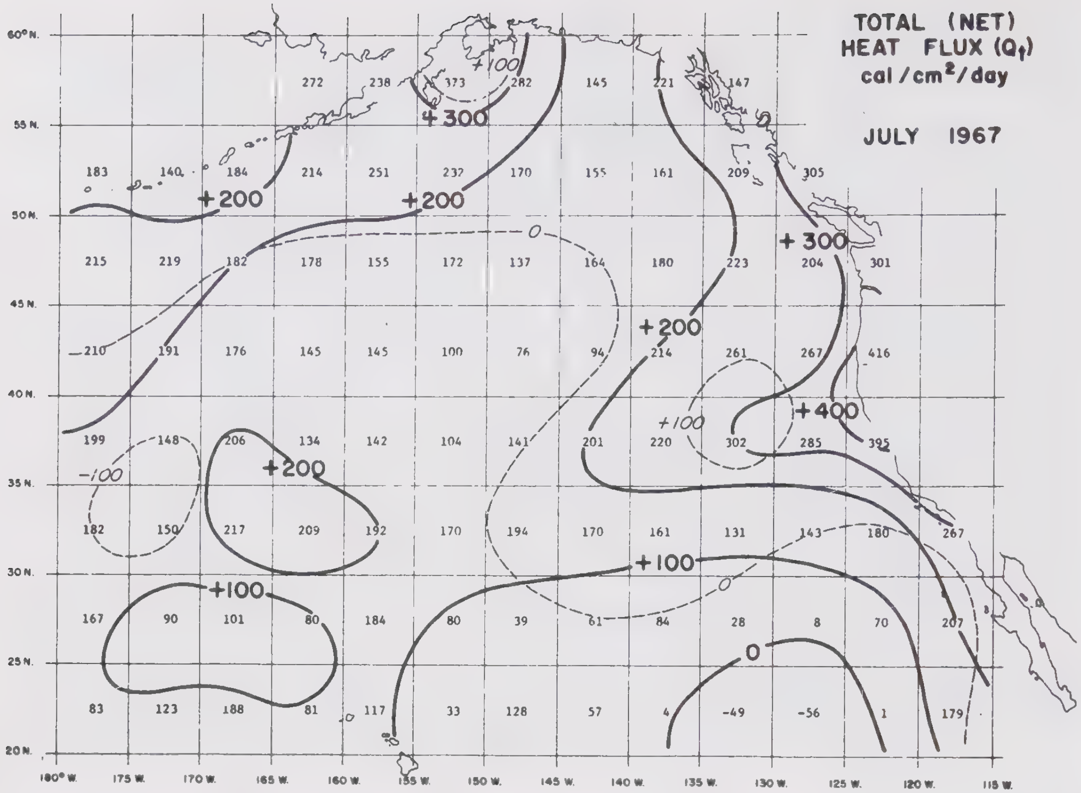
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

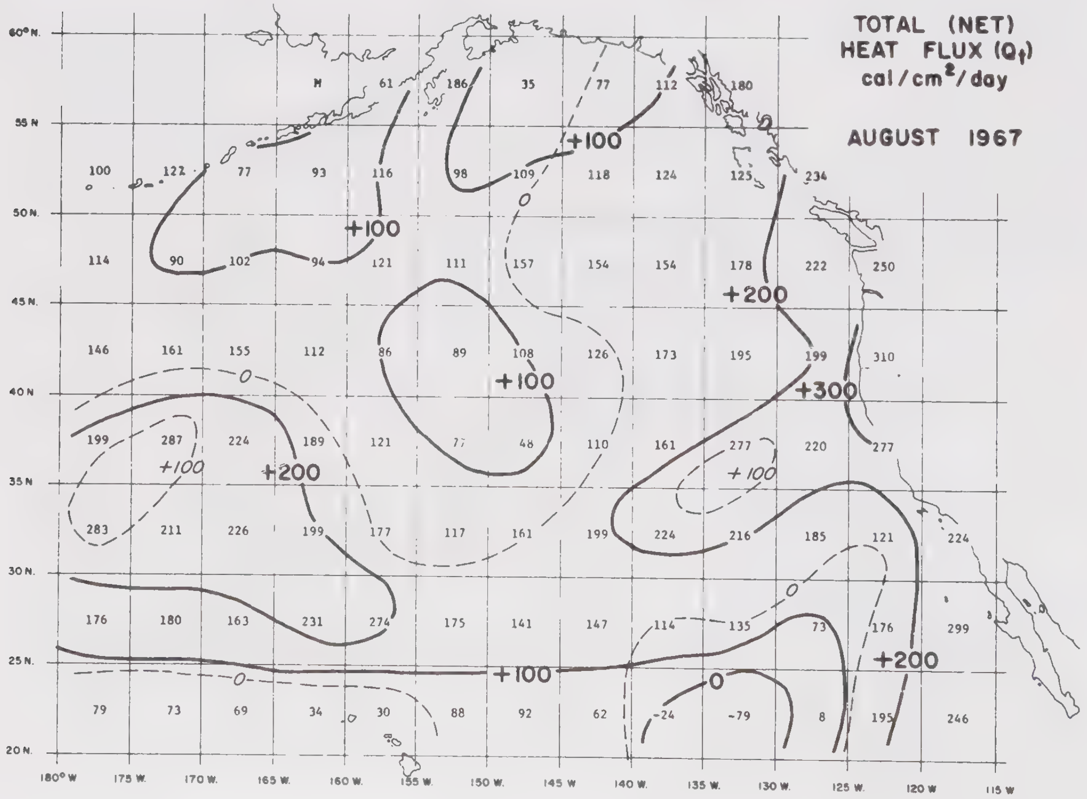
APRIL 1967

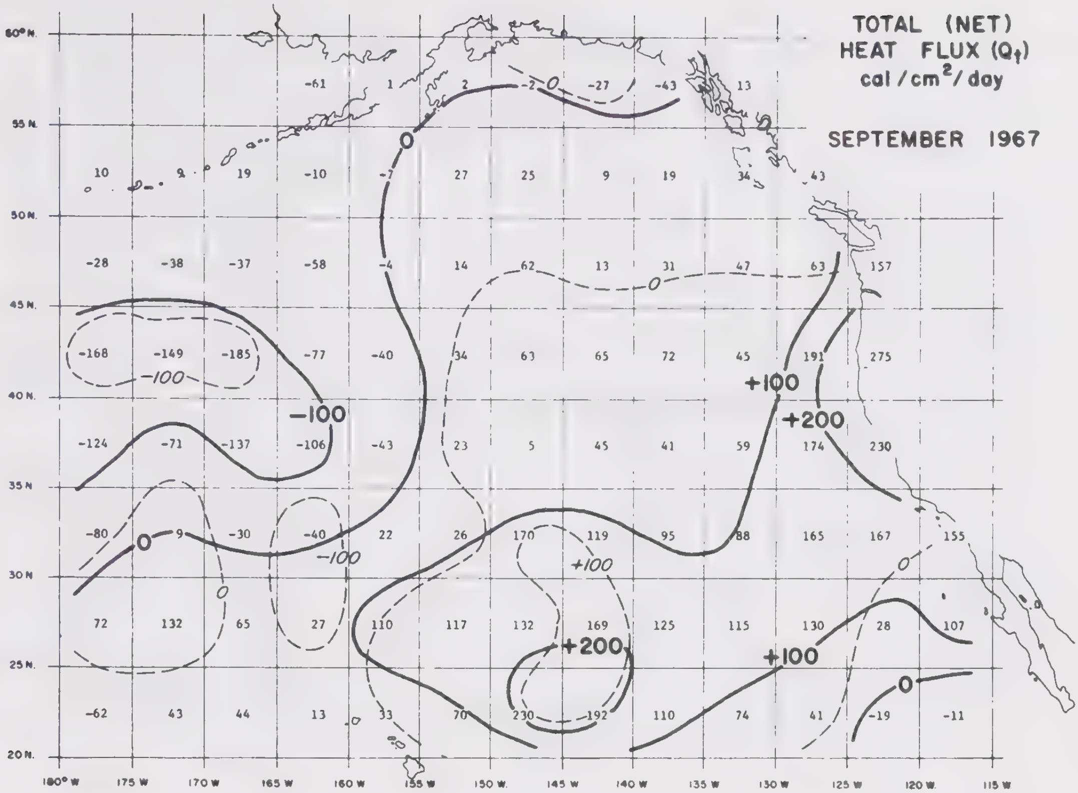
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W.
155 W
150 W
145 W
140 W
135 W
130 W
125 W.
120 W.
115 W.
53
151
163
156
+100
168
-103
143
144
154
109
161
150
167
147
155
102
161
M
196
171
145
158
155
136
132
128
0
+100
79
103
128
196
78
112
73
99
77
90
33
13
-8
55
38
85
0
60
33
87
37
5
4
-22
-60
-100
-21
48
118
-100
-100
69
80
100
33
-27
-37
-50
-69
-54
-7
+100
65
147
222
+200
-100
148
29
47
-61
104
-54
-54
-108
-80
-37
15
89
152
+100
+100
0
49
111
33
30
43
109
89
54
-57
-32
-97
-100
-90
-96

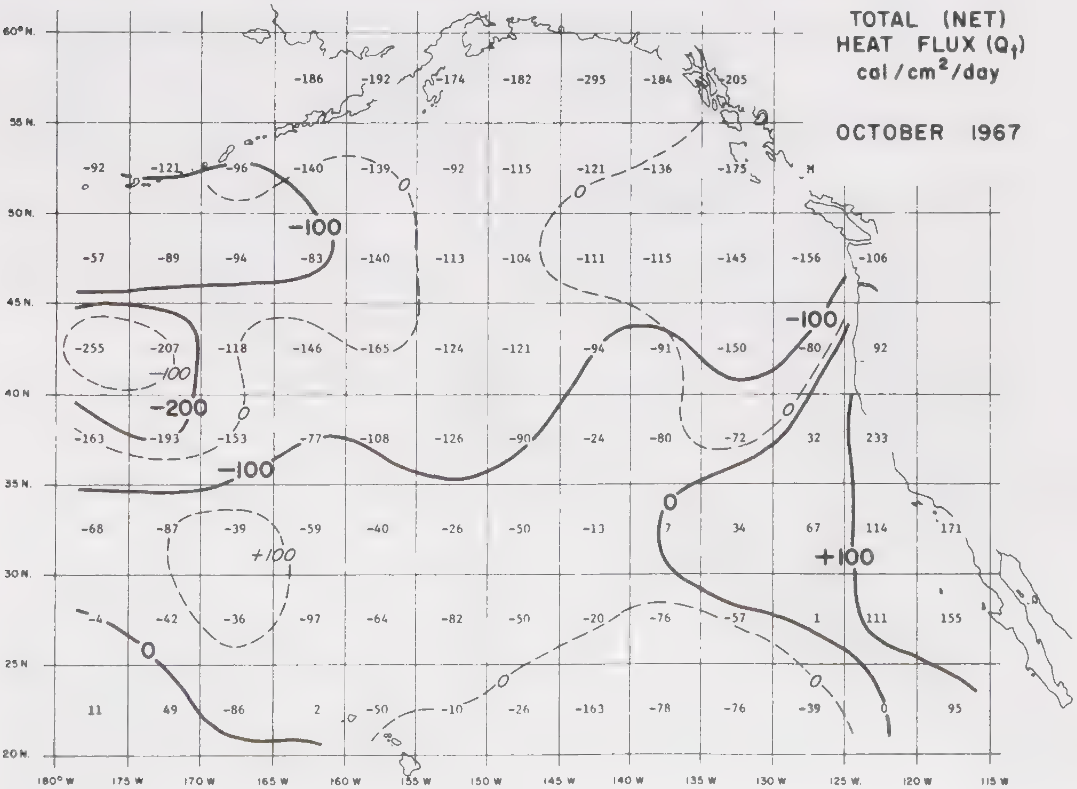

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
MAY 1967
126 120 254 223 146 88 181
127 140 166 175 240 177 169 168 178 210 203
141 143 150 137 171 170 187 187 191 163 161 229
71 94 96 125 107 130 177 170 177 165 187 246
109 102 68 124 142 187 117 129 136 120 173 273
90 86 125 124 150 160 158 159 84 99 117 172 282
192 151 112 111 158 187 82 33 25 61 73 114 242
-11 77 188 214 152 77 116 66 -20 -22 -11 63 174
+200
0
+200
+100
+100
+100
+100
0
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W

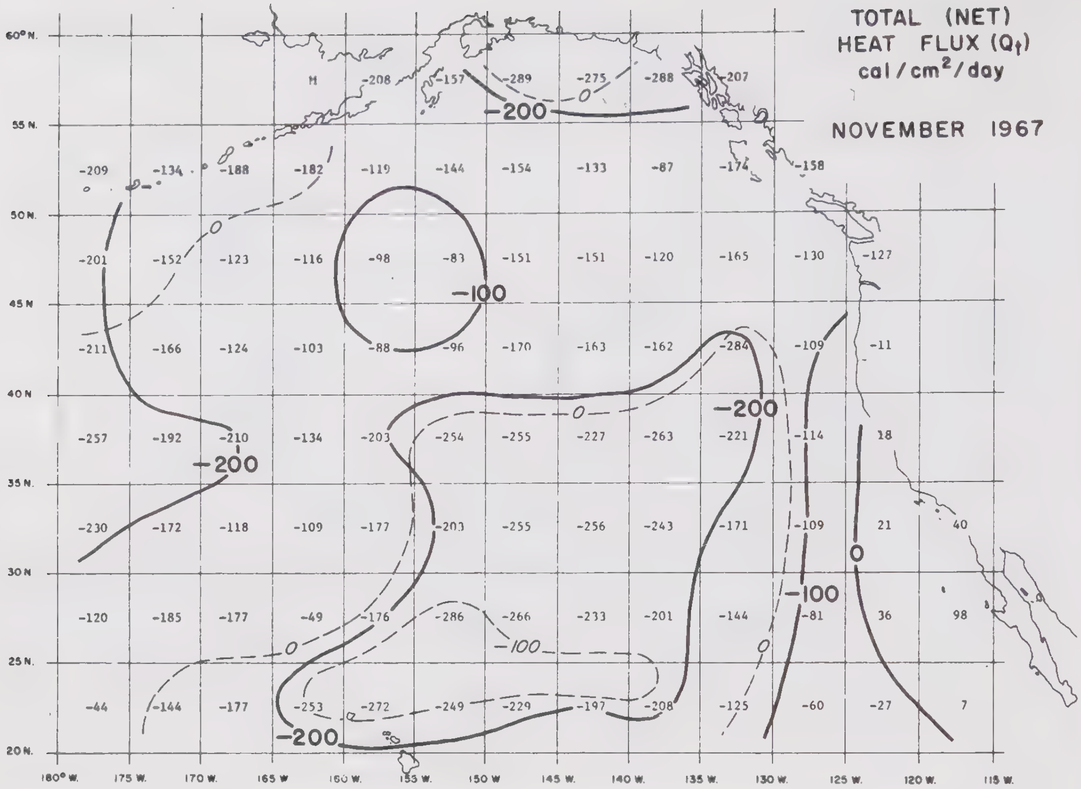

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
JUNE 1967
228 251 279 130 136 122 243
111 125 158 190 179 194 163 145 174 181 371
153 169 182 197 210 207 205 213 184 177 195 159
113 129 128 160 244 237 157 147 139 117 125 270
145 103 55 45 148 166 159 171 164 116 138 213
116 143 165 186 185 209 183 158 118 98 78 76 209
196 252 335 323 310 131 97 112 13 -48 -26 112 232
170 155 252 268 174 113 150 92 6 26 -25 21 111
0
+200
+200
0
-100
+100
-100
+200
+200
+300
0
+100
+100
0
-100
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W
125 W
120 W
115 W

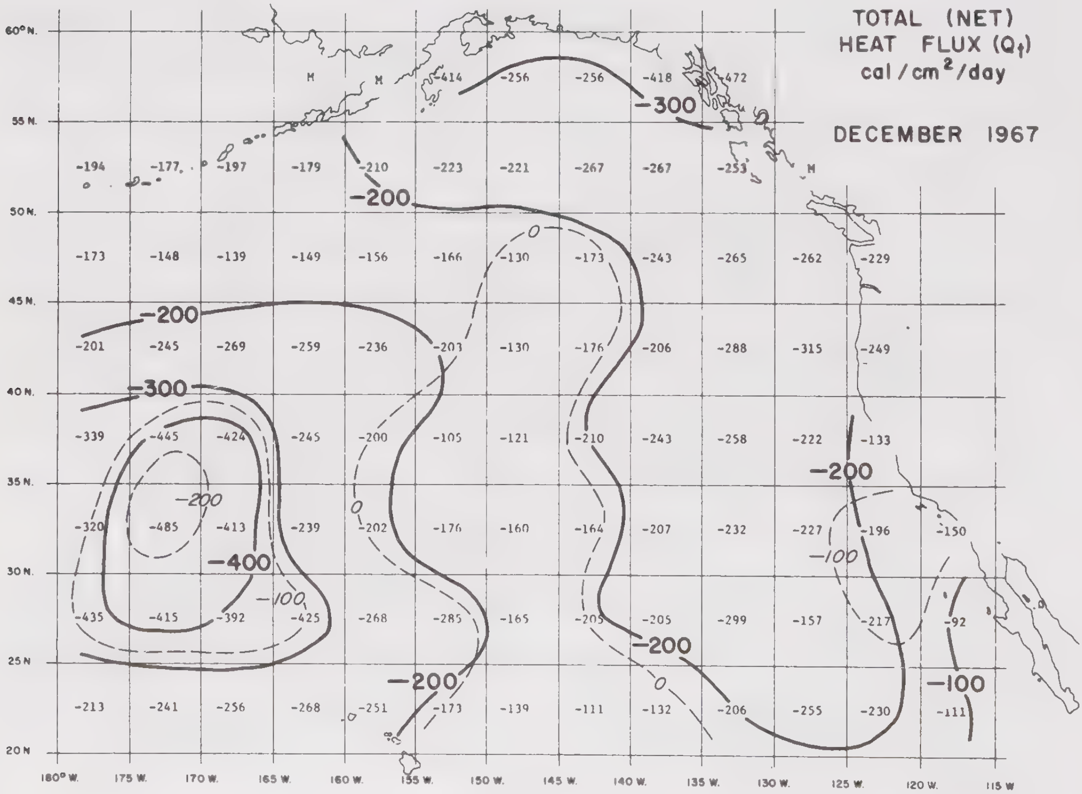

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
JULY 1967
272 238 373 282 145 221 147
183 140 184 214 251 232 170 155 161 209 305
215 219 182 178 155 172 137 164 180 223 204 301
210 191 176 145 145 100 76 94 214 261 267 416
199 148 206 134 142 104 141 201 220 302 285 395
182 150 217 209 192 170 194 170 161 131 143 180 267
167 90 101 80 184 80 39 61 84 28 8 70 207
83 123 188 81 117 33 128 57 4 -49 -56 1 179
+100
+300
+200
+200
0
+300
+200
+100
+400
-100
+200
+100
+100
0
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

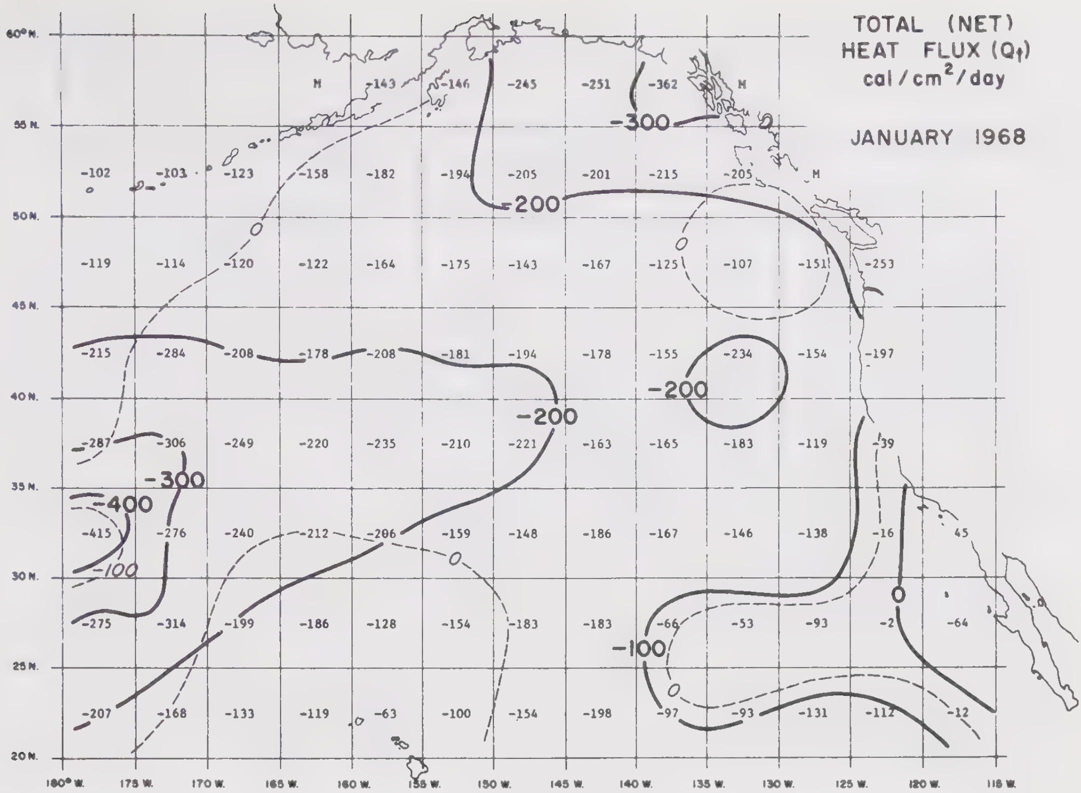

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
AUGUST 1967
M 61 186 35 77 112 180
100 122 77 93 116 98 109 118 124 125 234
114 90 102 94 121 111 157 154 154 178 222 250
146 161 155 112 86 89 108 126 173 195 199 310
199 287 224 189 121 77 48 110 161 277 220 277
283 211 226 199 177 117 161 199 224 216 185 121 224
176 180 163 231 274 175 141 147 114 135 73 176 299
79 73 69 34 30 88 92 62 -24 -79 8 195 246
+100
+100
0
+200
+100
0
+300
+100
+200
+100
0
+200
+100
0
0
60° N.
55 N
50 N.
45 N.
40 N
35 N
30 N.
25 N.
20 N.
180° W
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W
140 W.
135 W.
130 W.
125 W.
120 W
115 W


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
SEPTEMBER 1967
60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N.
25 N.
20 N.
180° W
175 W
170 W
165 W
160 W
155 W
150 W.
145 W
140 W
135 W
130 W
125 W
120 W.
115 W
-61 1 2 -2 -27 -43 13
10 19 -10 -7 27 25 9 19 34 43
-28 -38 -37 -58 -4 14 62 13 31 47 63 157
-168 -149 -185 -77 -40 34 63 65 72 45 191 275
-124 -71 -137 -106 -43 23 5 45 41 59 174 230
-80 9 -30 -40 22 26 170 119 95 88 165 167 155
72 132 65 27 110 117 132 169 125 115 130 28 107
-62 43 44 13 33 70 230 192 110 74 41 -19 -11
0
-100
+100
+200


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
OCTOBER 1967
60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N.
25 N
20 N.
180° W
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W.
120 W
115 W
-186 -192 -174 -182 -295 -184 -205
-92 -121 -96 -140 -139 -92 -115 -121 -136 -175
-57 -89 -94 -83 -140 -113 -104 -111 -115 -145 -156 -106
-255 -207 -118 -146 -165 -124 -121 -94 -91 -150 -80 92
-163 -193 -153 -77 -108 -126 -90 -24 -80 -72 32 233
-68 -87 -39 -59 -40 -26 -50 -13 7 34 67 114 171
-4 -42 -36 -97 -64 -82 -50 -20 -76 -57 1 111 155
11 49 -86 2 -50 -10 -26 -163 -78 -76 -39 0 95
0
-100
-200
+100

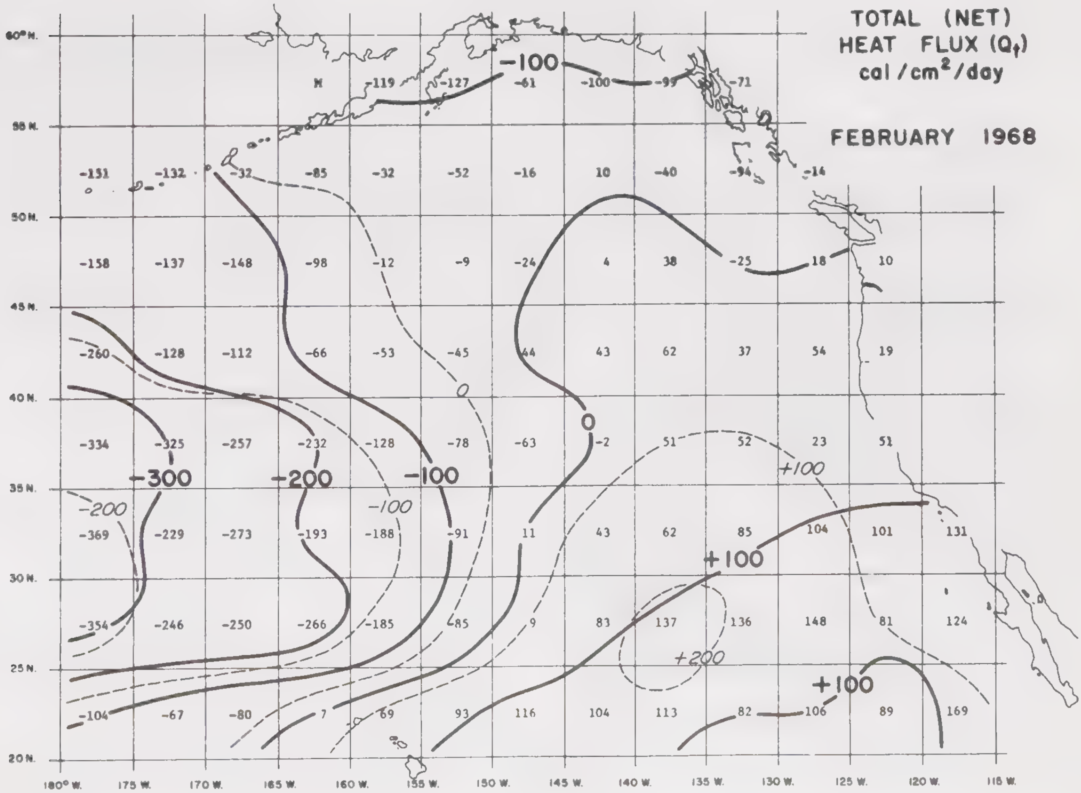

TOTAL (NET) HEAT FLUX (Q_t) cal / cm² / day
NOVEMBER 1967
60° N.
55 N.
50 N.
45 N
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W
160 W.
155 W.
150 W
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -208 -157 -289 -275 -288 -207
-209 -134 -188 -182 -119 -144 -154 -133 -87 -174 -158
-201 -152 -123 -116 -98 -83 -151 -151 -120 -165 -130 -127
-211 -166 -124 -103 -88 -96 -170 -163 -162 -284 -109 -11
-257 -192 -210 -134 -203 -254 -255 -227 -263 -221 -114 18
-230 -172 -118 -109 -177 -203 -255 -256 -243 -171 -109 21 40
-120 -185 -177 -49 -176 -286 -266 -233 -201 -144 -81 36 98
-44 -144 -177 -253 -272 -249 -229 -197 -208 -125 -60 -27 7
-200
0
-100
-200
-200
0
-200
0
-100
0
-100
0
-200


TOTAL (NET) HEAT FLUX (Q_t) cal / cm² / day
DECEMBER 1967
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M M -414 -256 -256 -418 -472
-194 -177 -197 -179 -210 -223 -221 -267 -267 -253 M
-173 -148 -139 -149 -156 -166 -130 -173 -243 -265 -262 -229
-201 -245 -269 -259 -236 -203 -130 -176 -206 -288 -315 -249
-339 -445 -424 -245 -200 -105 -121 -210 -243 -258 -222 -133
-320 -485 -413 -239 -202 -176 -160 -164 -207 -232 -227 -196 -150
-435 -415 -392 -425 -268 -285 -165 -205 -205 -299 -157 -217 -92
-213 -241 -256 -268 -251 -173 -139 -111 -132 -206 -255 -230 -111
-300
-200
0
-200
-300
-200
-400
-100
0
-200
-200
0
-200
-100
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

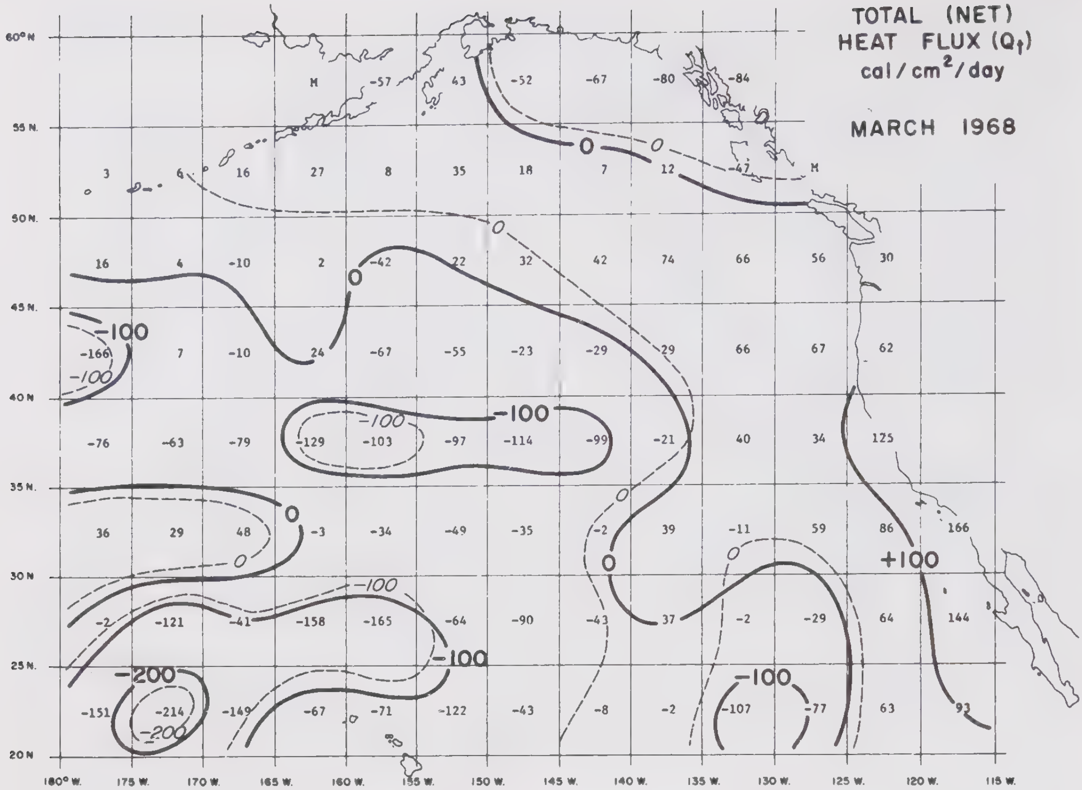
JANUARY 1968

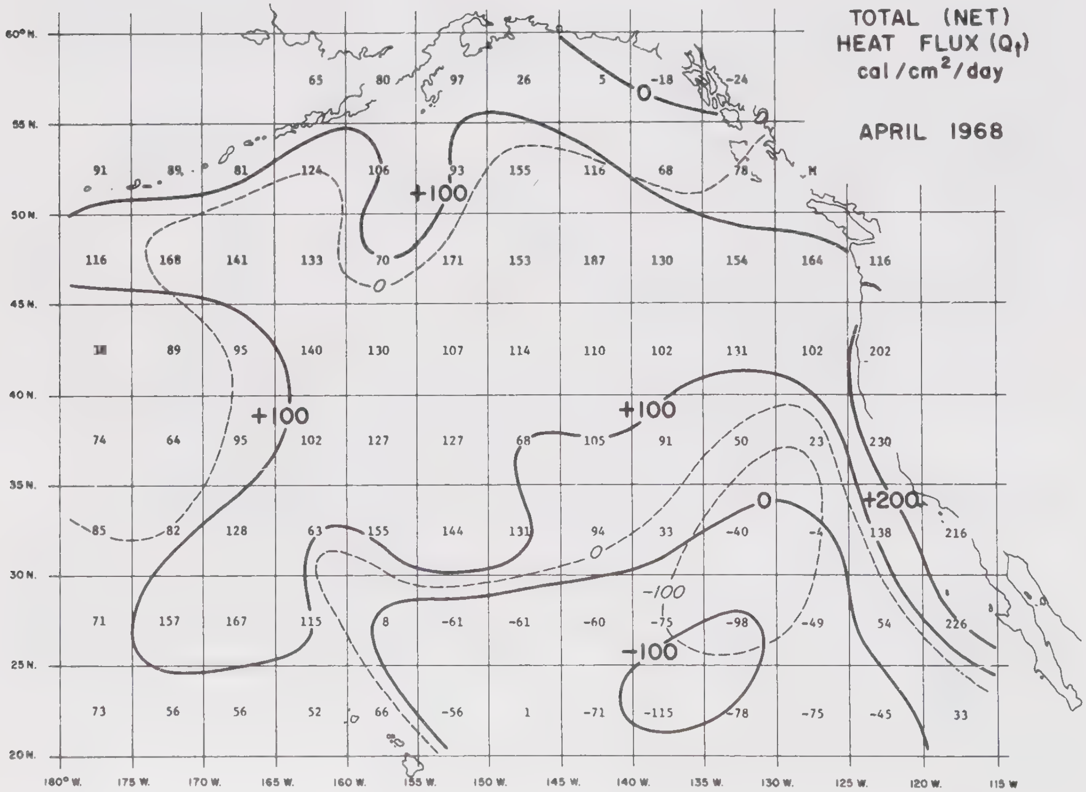
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -143 -146 -245 -251 -362 M
-300
-102 -103 -123 -158 -182 -194 -205 -201 -215 -205 M
-200
0
-119 -114 -120 -122 -164 -175 -143 -167 -125 -107 -151 -253
-215 -284 -208 -178 -208 -181 -194 -178 -155 -234 -154 -197
-200
-200
-287 -306 -249 -220 -235 -210 -221 -163 -165 -183 -119 -39
-300
-400
-415 -276 -240 -212 -206 -159 -148 -186 -167 -146 -138 -16 45
-100
0
0
-275 -314 -199 -186 -128 -154 -183 -183 -66 -53 -93 -2 -64
-100
0
-207 -168 -133 -119 -63 -100 -154 -198 -97 -93 -131 -112 -12

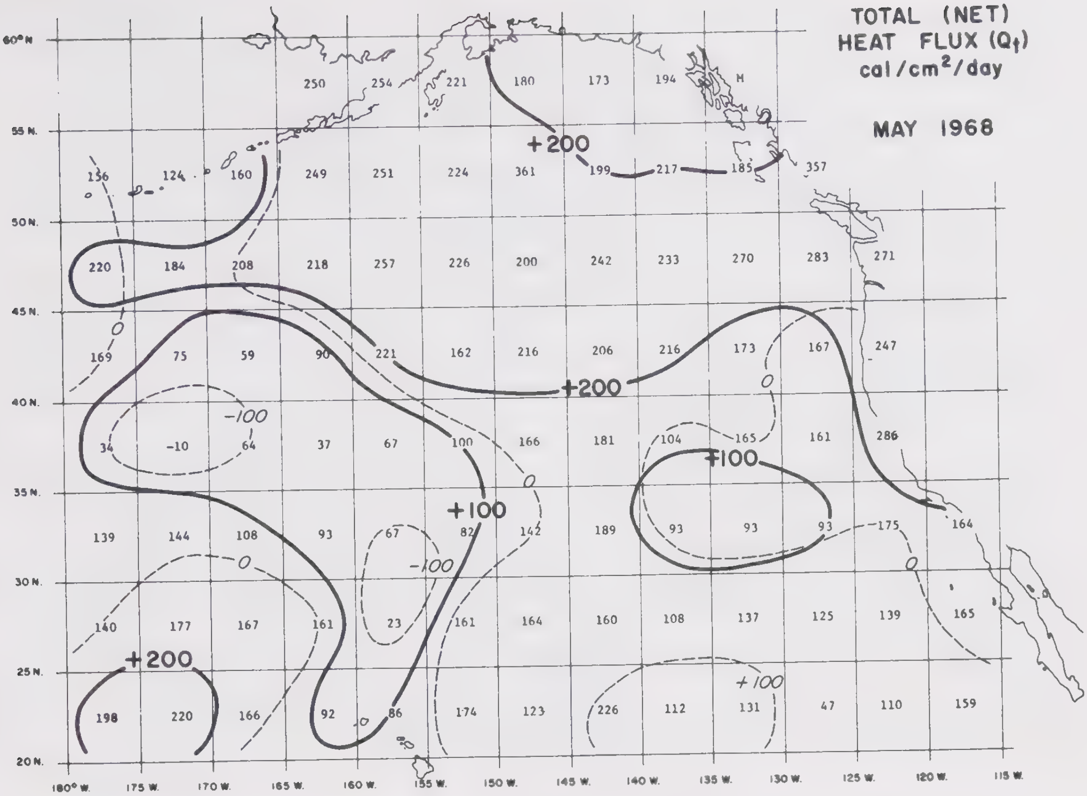

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

FEBRUARY 1968

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -119 -127 -61 -100 -99 -71
-100
-131 -132 -32 -85 -32 -52 -16 10 -40 -94 -14
-158 -137 -148 -98 -12 -9 -24 4 38 -25 18 10
-260 -128 -112 -66 -53 -45 44 43 62 37 54 19
0
0
-334 -325 -257 -232 -128 -78 -63 -2 51 52 23 51
+100
-300
-200
-100
-200
-100
-369 -229 -273 -193 -188 -91 11 43 62 85 104 101 131
+100
-354 -246 -250 -266 -185 -85 9 83 137 136 148 81 124
+200
+100
-104 -67 -80 7 69 93 116 104 113 82 106 89 169


TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
MARCH 1968
60° N
55 N.
50 N.
45 N.
40 N
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
-57
43
-52
-67
-80
-84
0
0
3
6
16
27
8
35
18
7
12
-47
M
0
16
4
-10
2
-42
22
32
42
74
66
56
30
0
-100
-166
7
-10
24
-67
-55
-23
-29
29
66
67
62
-100
-100
-100
-76
-63
-79
-129
-103
-97
-114
-99
-21
40
34
125
0
0
36
29
48
-3
-34
-49
-35
-2
39
-11
59
86
166
0
0
0
+100
-100
-2
-121
-41
-158
-165
-64
-90
-43
37
-2
-29
64
144
-100
-200
-100
-151
-214
-149
-67
-71
-122
-43
-8
-2
-107
-77
63
93
-200

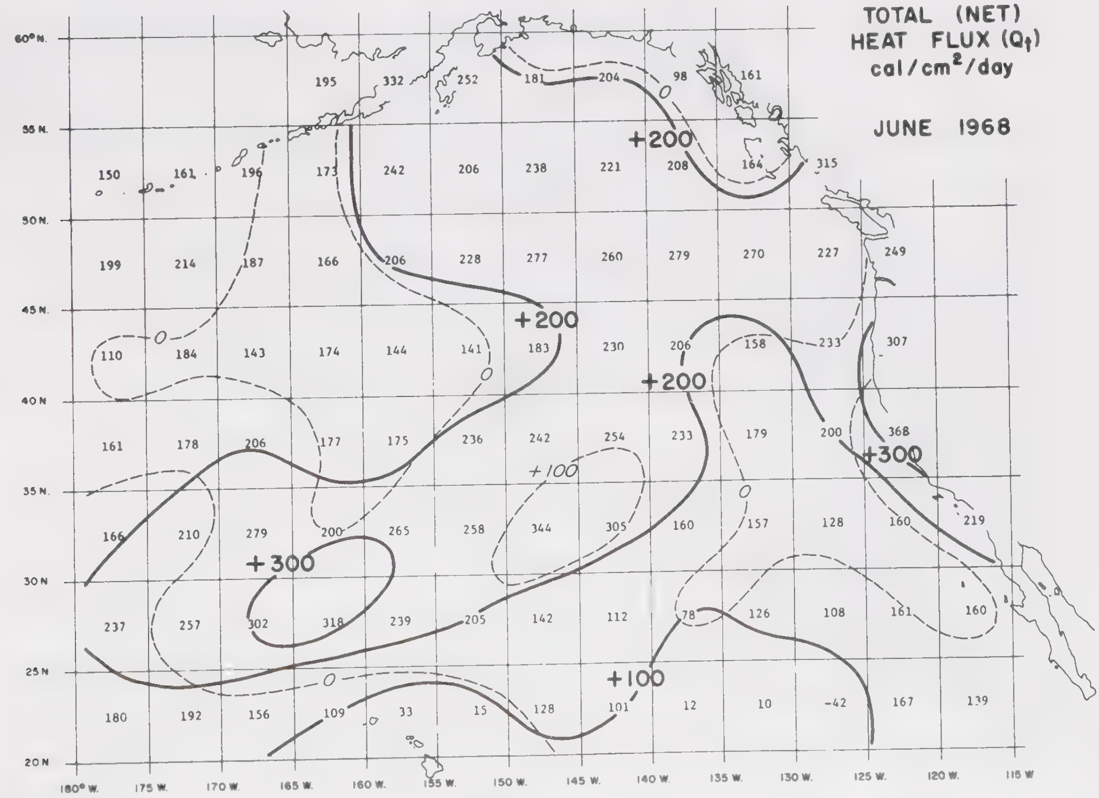

TOTAL (NET)
HEAT FLUX (Q_t)
cal/cm²/day
APRIL 1968
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
65
80
97
26
5
0
-18
-24
91
89
81
124
106
93
155
116
68
78
M
+100
116
168
141
133
70
171
153
187
130
154
164
116
0
89
95
140
130
107
114
110
102
131
102
202
+100
+100
74
64
95
102
127
127
68
105
91
50
23
230
0
+200
85
82
128
63
155
144
131
94
33
-40
-4
138
216
0
-100
71
157
167
115
8
-61
-61
-60
-75
-98
-49
54
226
-100
73
56
56
52
66
-56
1
-71
-115
-78
-75
-45
33



TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day

MAY 1968

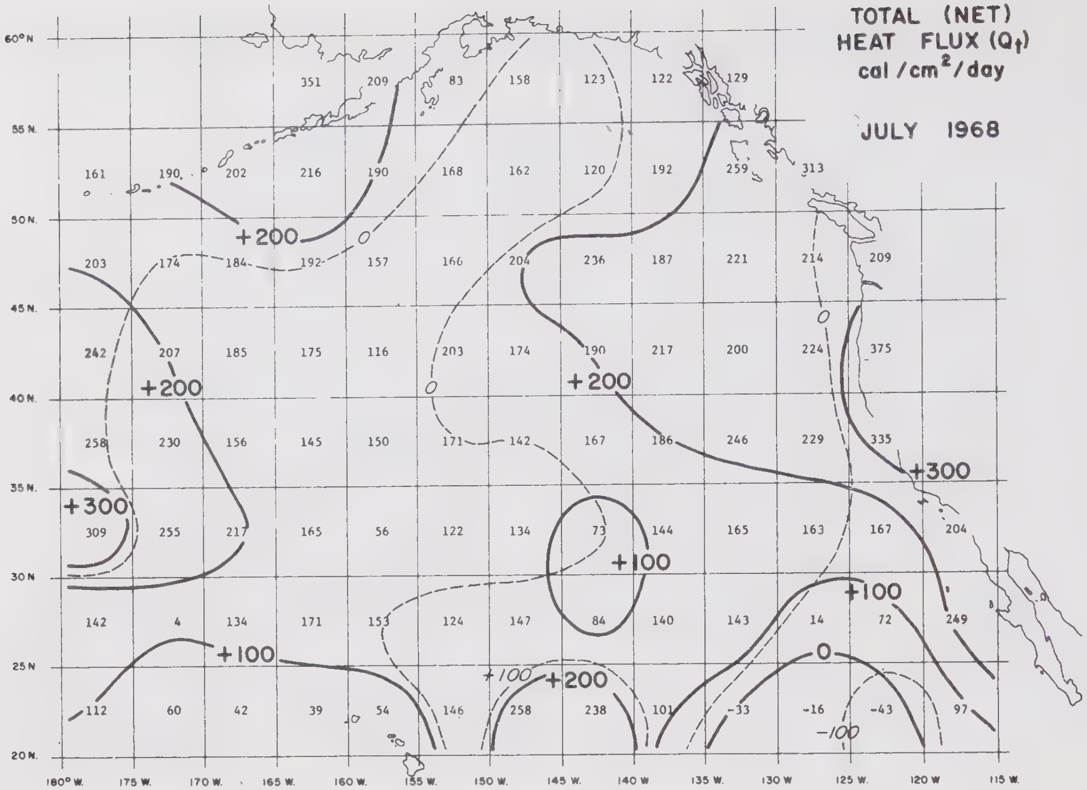
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
250 254 221 180 173 194
M
+200
156 124 160 249 251 224 361 199 217 185 357
220 184 208 218 257 226 200 242 233 270 283 271
0
169 75 59 90 221 162 216 206 216 173 167 247
+200
0
-100
34 -10 64 37 67 100 166 181 104 165 161 286
+100
0
+100
139 144 108 93 67 82 142 189 93 93 93 175 164
0
-100
0
140 177 167 161 23 161 164 160 108 137 125 139 165
+200
+100
198 220 166 92 86 174 123 226 112 131 47 110 159

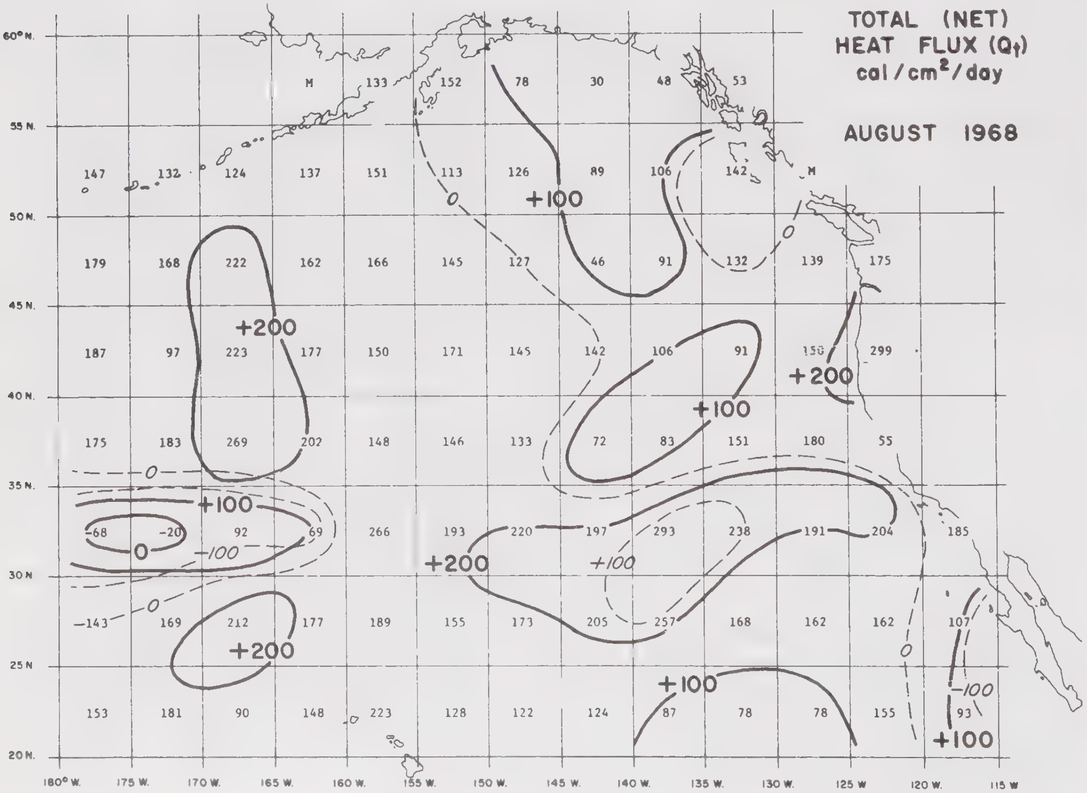


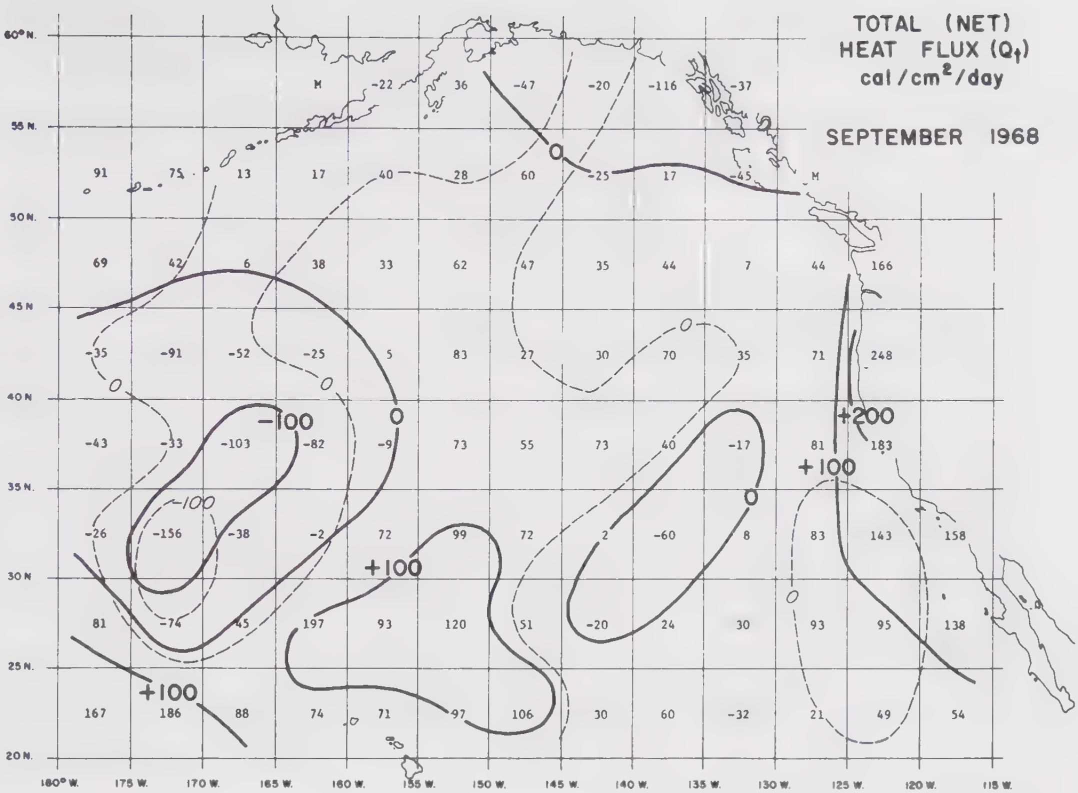
TOTAL (NET) HEAT FLUX (Q_t)
cal/cm²/day

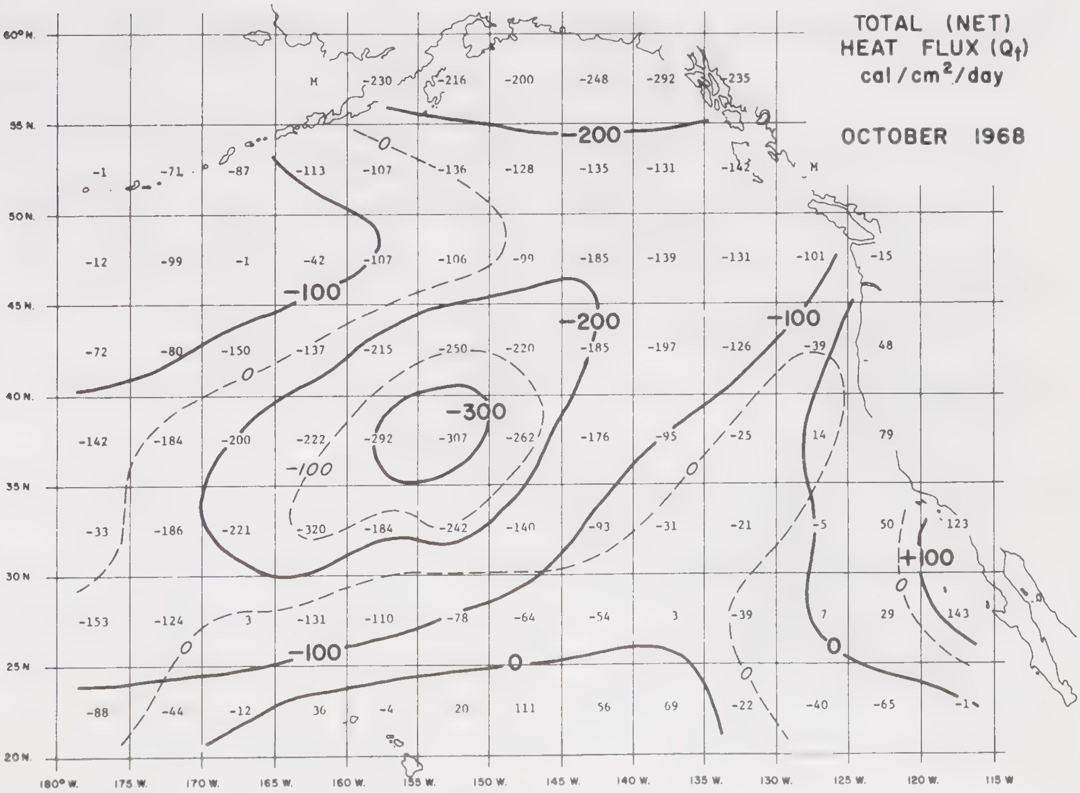
JUNE 1968

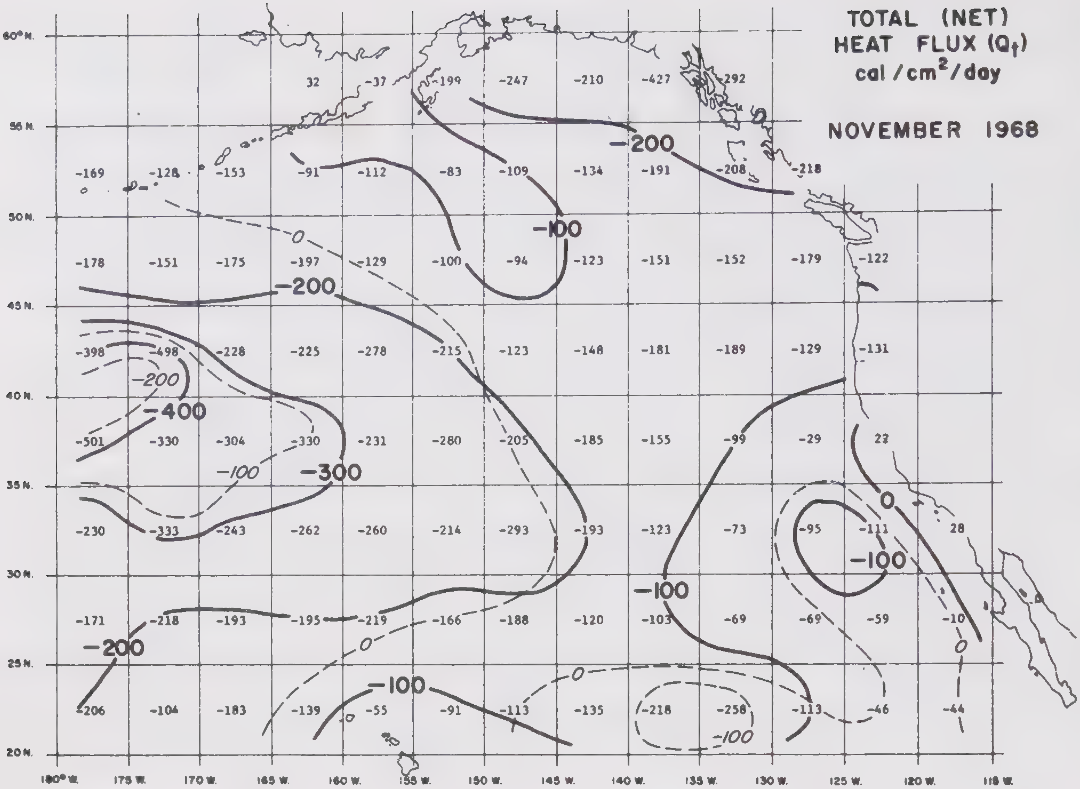
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
195 332 252 181 204 98 161
0
+200
150 161 196 173 242 206 238 221 208 164 315
199 214 187 166 206 228 277 260 279 270 227 249
+200
0
110 184 143 174 144 141 183 230 206 158 233 307
0
+200
161 178 206 177 175 236 242 254 233 179 200 368
+300
+100
0
166 210 279 200 265 258 344 305 160 157 128 160 219
+300
237 257 302 318 239 205 142 112 78 126 108 161 160
+100
0
180 192 156 109 33 15 128 101 12 10 -42 167 139


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
JULY 1968
60°N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W
135 W.
130 W
125 W.
120 W
115 W.
351 209 83 158 123 122 129
161 190 202 216 190 168 162 120 192 259 313
203 174 184 192 157 166 204 236 187 221 214 209
242 207 185 175 116 203 174 190 217 200 224 375
258 230 156 145 150 171 142 167 186 246 229 335
309 255 217 165 56 122 134 73 144 165 163 167 204
142 4 134 171 153 124 147 84 140 143 14 72 249
112 60 42 39 54 146 258 238 101 -33 -16 -43 97
+200
0
+200
+200
0
+300
+300
+100
+100
+100
+100
+200
0
0
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
AUGUST 1968
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W
120 W.
115 W
M 133 152 78 30 48 53
147 132 124 137 151 113 126 89 106 142 M
179 168 222 162 166 145 127 46 91 132 139 175
187 97 223 177 150 171 145 142 106 91 150 299
175 183 269 202 148 146 133 72 83 151 180 55
-68 -20 92 69 266 193 220 197 293 238 191 204 185
-143 169 212 177 189 155 173 205 257 168 162 162 107
153 181 90 148 223 128 122 124 87 78 78 155 93
0
+100
0
+100
0
-100
0
+200
+200
+200
+100
+100
+200
+100
0
-100
+100

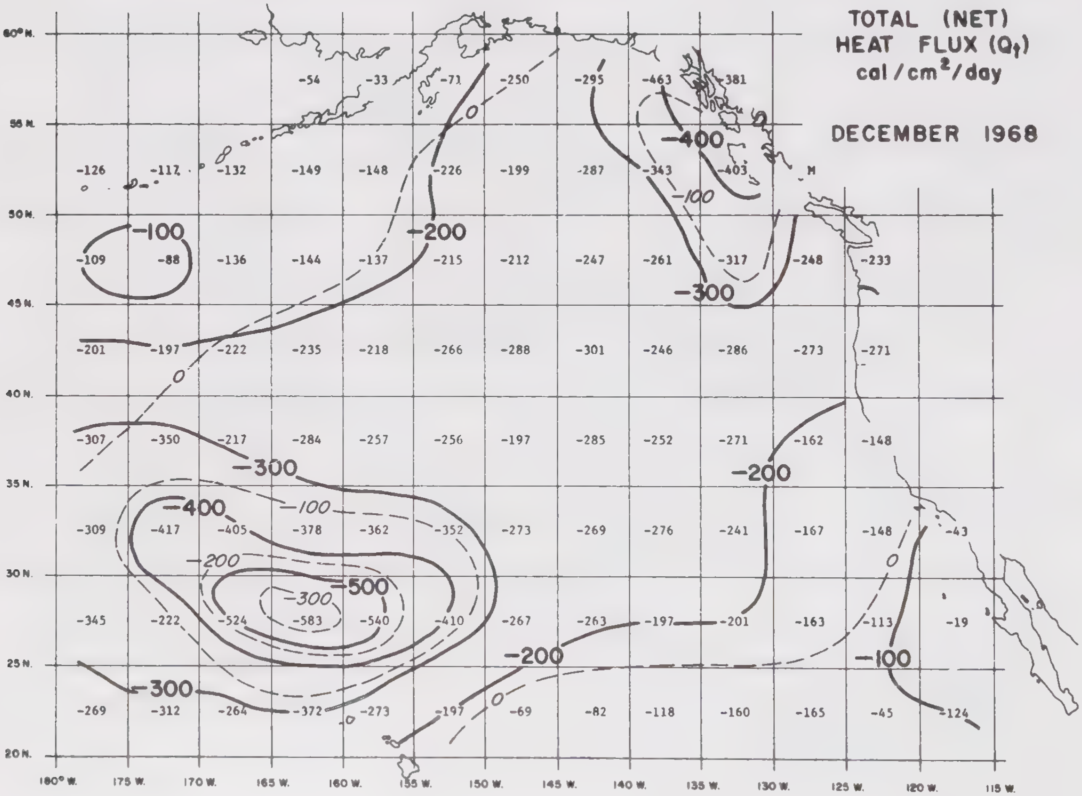

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
SEPTEMBER 1968
M -22 36 -47 -20 -116 -37
91 75 13 17 40 28 60 -25 17 -45 M
69 42 6 38 33 62 47 35 44 7 44 166
-35 -91 -52 -25 5 83 27 30 70 35 71 248
-43 -33 -103 -82 -9 73 55 73 40 -17 81 183
-26 -156 -38 -2 72 99 72 2 -60 8 83 143 158
81 -74 45 197 93 120 51 -20 24 30 93 95 138
167 186 88 74 71 97 106 30 60 -32 21 49 54
0
-100
+100
+200
60° N.
55 N.
50 N.
45 N
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
OCTOBER 1968
M -230 -216 -200 -248 -292 -235
-1 -71 -87 -113 -107 -136 -128 -135 -131 -142 M
-12 -99 -1 -42 -107 -106 -99 -185 -139 -131 -101 -15
-72 -80 -150 -137 -215 -250 -220 -185 -197 -126 -39 48
-142 -184 -200 -222 -292 -307 -262 -176 -95 -25 14 79
-33 -186 -221 -320 -184 -242 -140 -93 -31 -21 -5 50 123
-153 -124 3 -131 -110 -78 -64 -54 3 -39 7 29 143
-88 -44 -12 36 -4 20 111 56 69 -22 -40 -65 -1
0
-100
-200
-300
+100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

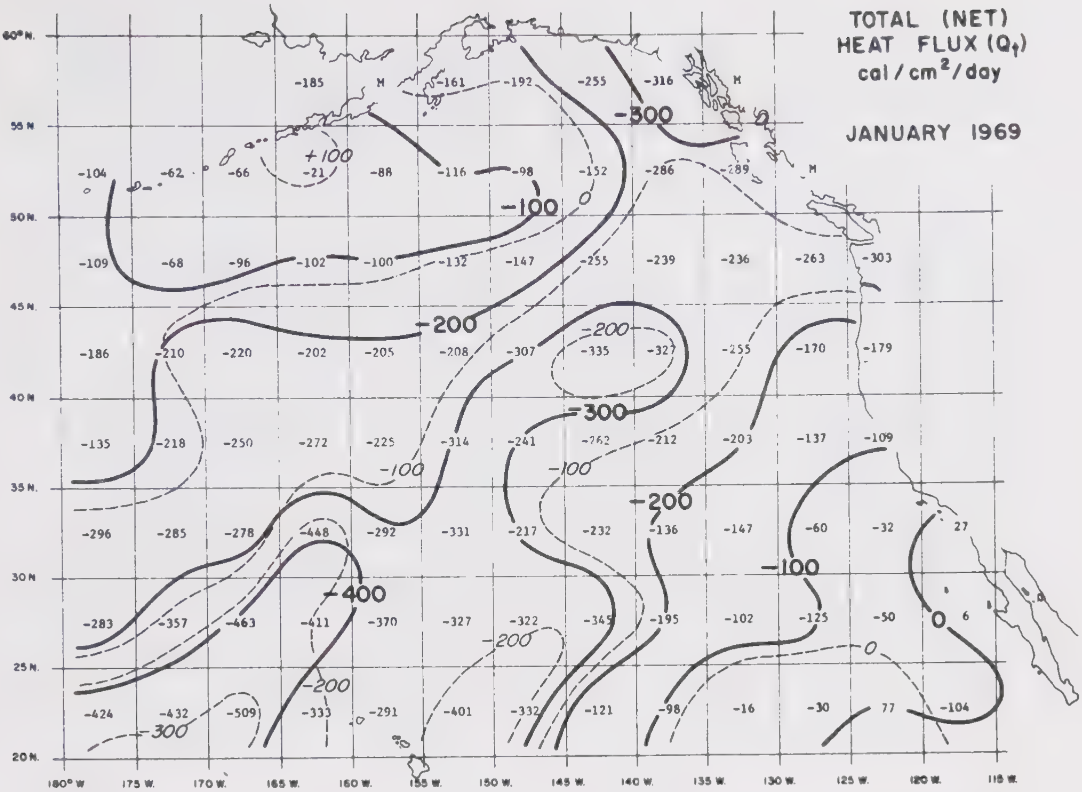
NOVEMBER 1968

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
32 -37 -199 -247 -210 -427 -292
-169 -128 -153 -91 -112 -83 -109 -134 -191 -208 -218
-178 -151 -175 -197 -129 -100 -94 -123 -151 -152 -179 -122
-398 -498 -228 -225 -278 -215 -123 -148 -181 -189 -129 -131
-501 -330 -304 -330 -231 -280 -205 -185 -155 -99 -29 22
-230 -333 -243 -262 -260 -214 -293 -193 -123 -73 -95 -111 28
-171 -218 -193 -195 -219 -166 -188 -120 -103 -69 -69 -59 -10
-206 -104 -183 -139 -55 -91 -113 -135 -218 -258 -113 -46 -44
-200
-100
0
-200
-200
-400
-100
-300
-200
-100
0
-100
-100
0
0
-100
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

DECEMBER 1968

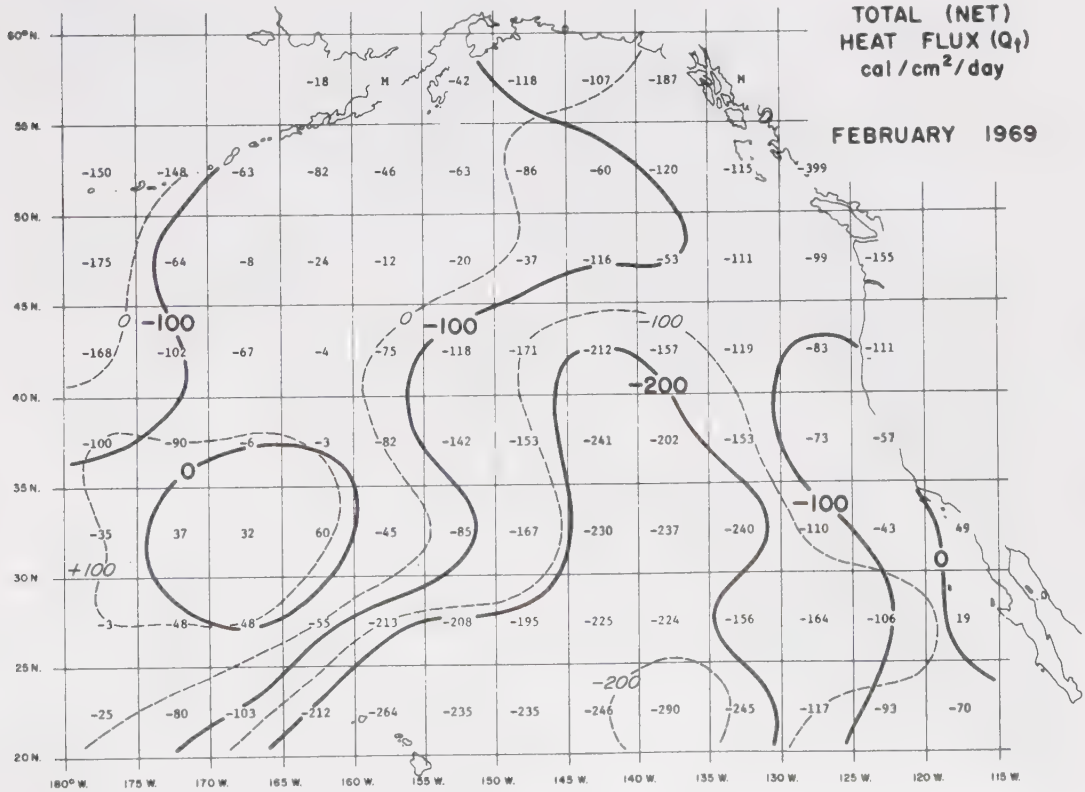
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-54 -33 -71 -250 -295 -463 -381
-126 -117 -132 -149 -148 -226 -199 -287 -343 -403
-109 -88 -136 -144 -137 -215 -212 -247 -261 -317 -248 -233
-201 -197 -222 -235 -218 -266 -288 -301 -246 -286 -273 -271
-307 -350 -217 -284 -257 -256 -197 -285 -252 -271 -162 -148
-309 -417 -405 -378 -362 -352 -273 -269 -276 -241 -167 -148 -43
-345 -222 -524 -583 -540 -410 -267 -263 -197 -201 -163 -113 -19
-269 -312 -264 -372 -273 -197 -69 -82 -118 -160 -165 -45 -124
0
-400
-100
-100
-200
-300
0
-300
-200
-400
-100
-200
-300
-500
0
-200
-300
-100
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JANUARY 1969

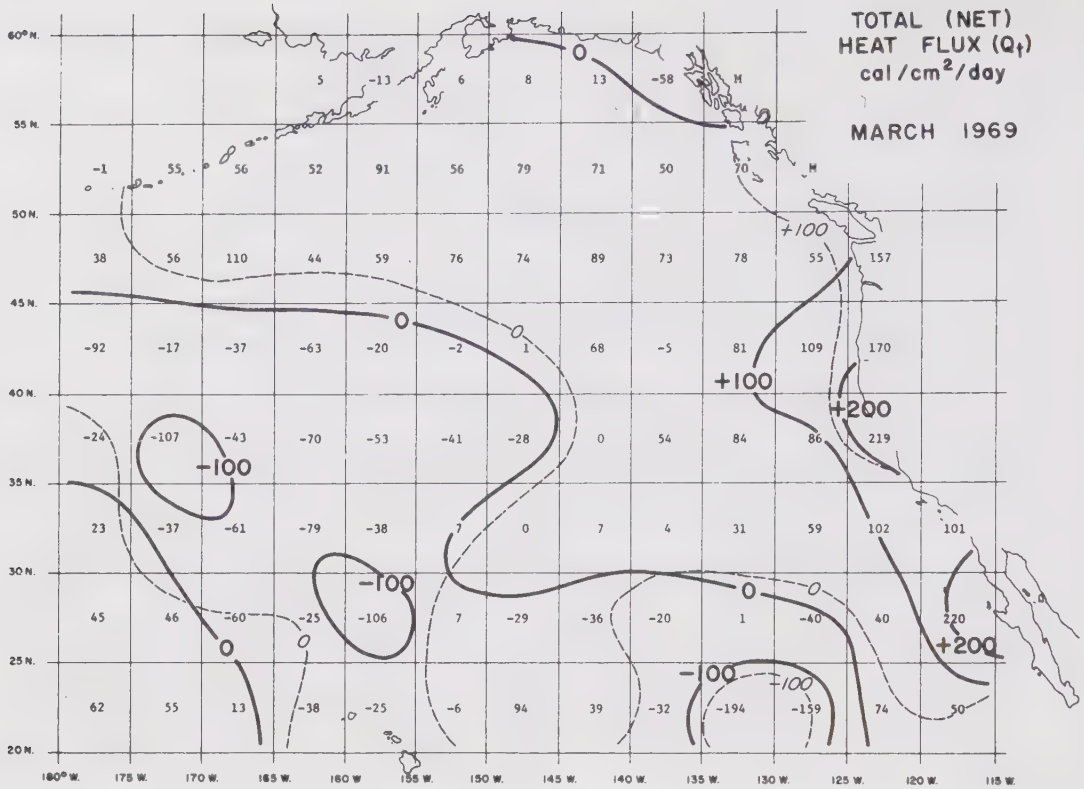
60° N.
55 N
50 N.
45 N.
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
-185 -161 -192 -255 -316
-104 -62 -66 -21 -88 -116 -98 -152 -286 -289
+100
-109 -68 -96 -102 -100 -132 -147 -255 -239 -236 -263 -303
-186 -210 -220 -202 -205 -208 -307 -335 -327 -255 -170 -179
-135 -218 -250 -272 -225 -314 -241 -262 -212 -203 -137 -109
-296 -285 -278 -448 -292 -331 -217 -232 -136 -147 -60 -32 27
-283 -357 -463 -411 -370 -327 -322 -345 -195 -102 -125 -50 6
-424 -432 -509 -333 -291 -401 -332 -121 -98 -16 -30 77 -104
-100
-200
-300
-400
0

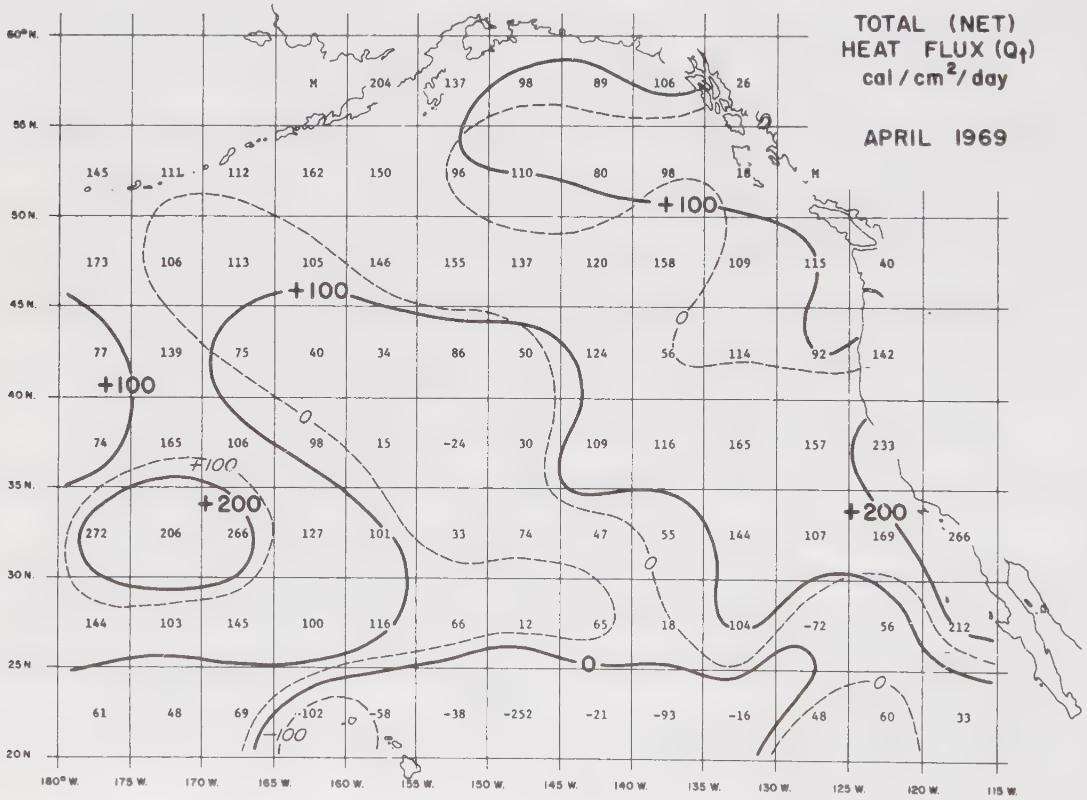


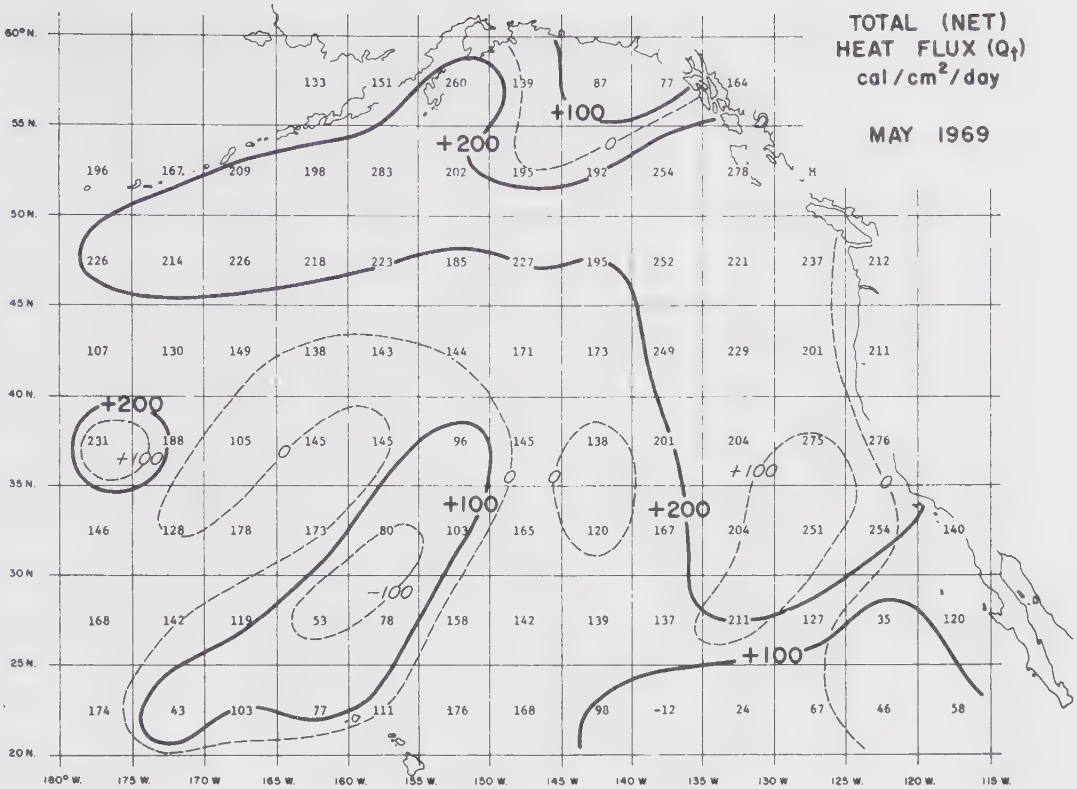
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

FEBRUARY 1969

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
-18 -42 -118 -107 -187
-150 -148 -63 -82 -46 -63 -86 -60 -120 -115 -399
-175 -64 -8 -24 -12 -20 -37 -116 -53 -111 -99 -155
-168 -102 -67 -4 -75 -118 -171 -212 -157 -119 -83 -111
-100 -90 -6 -3 -82 -142 -153 -241 -202 -153 -73 -57
-35 37 32 60 -45 -85 -167 -230 -237 -240 -110 -43 49
-3 -48 -48 -55 -213 -208 -195 -225 -224 -156 -164 -106 19
-25 -80 -103 -212 -264 -235 -235 -246 -290 -245 -117 -93 -70
+100
0
-100
-200

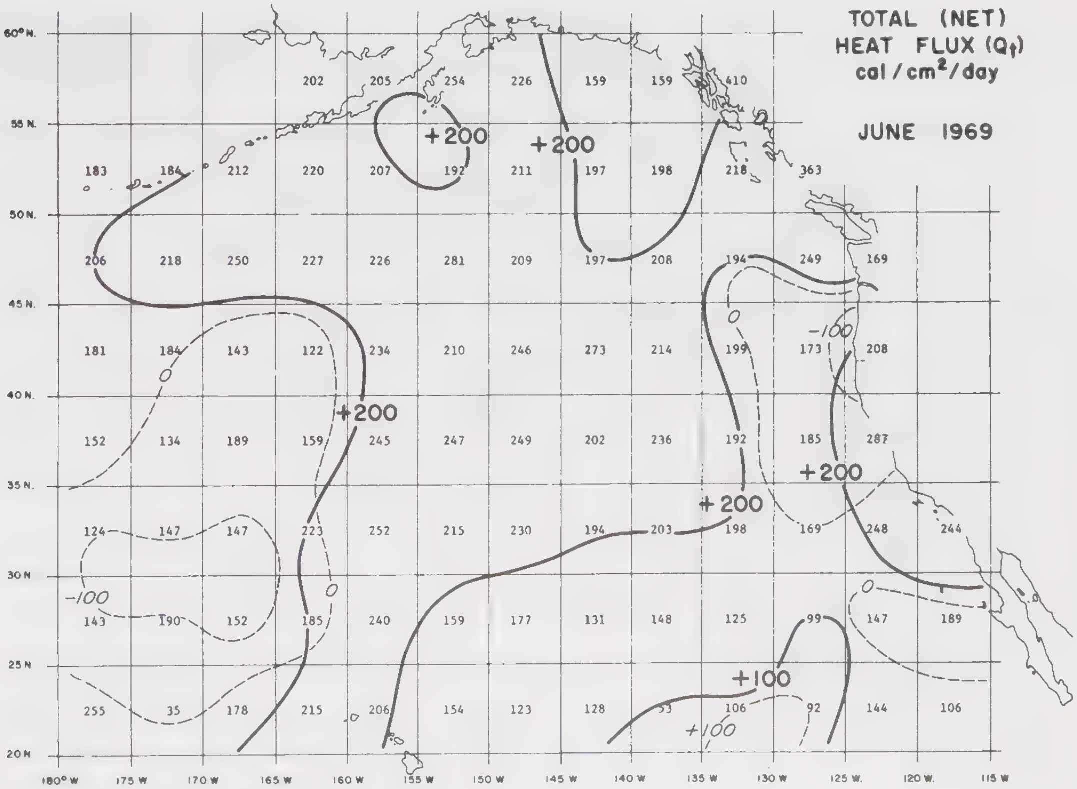

TOTAL (NET)
HEAT FLUX (Qt)
cal/cm²/day
MARCH 1969
5 -13 6 8 13 -58 M
-1 55 56 52 91 56 79 71 50 70 M
38 56 110 44 59 76 74 89 73 78 55 157
-92 -17 -37 -63 -20 -2 1 68 -5 81 109 170
-24 -107 -43 -70 -53 -41 -28 0 54 84 86 219
23 -37 -61 -79 -38 7 0 7 4 31 59 102 101
45 46 -60 -25 -106 7 -29 -36 -20 1 -40 40 220
62 55 13 -38 -25 -6 94 39 -32 -194 -159 74 50
0
+100
-100
+200
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET)
HEAT FLUX (Qt)
cal/cm²/day
APRIL 1969
M 204 137 98 89 106 26
145 111 112 162 150 96 110 80 98 18 M
173 106 113 105 146 155 137 120 158 109 115 40
77 139 75 40 34 86 50 124 56 114 92 142
74 165 106 98 15 -24 30 109 116 165 157 233
272 206 266 127 101 33 74 47 55 144 107 169 266
144 103 145 100 116 66 12 65 18 104 -72 56 212
61 48 69 -102 -58 -38 -252 -21 -93 -16 48 60 33
0
+100
+200
-100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

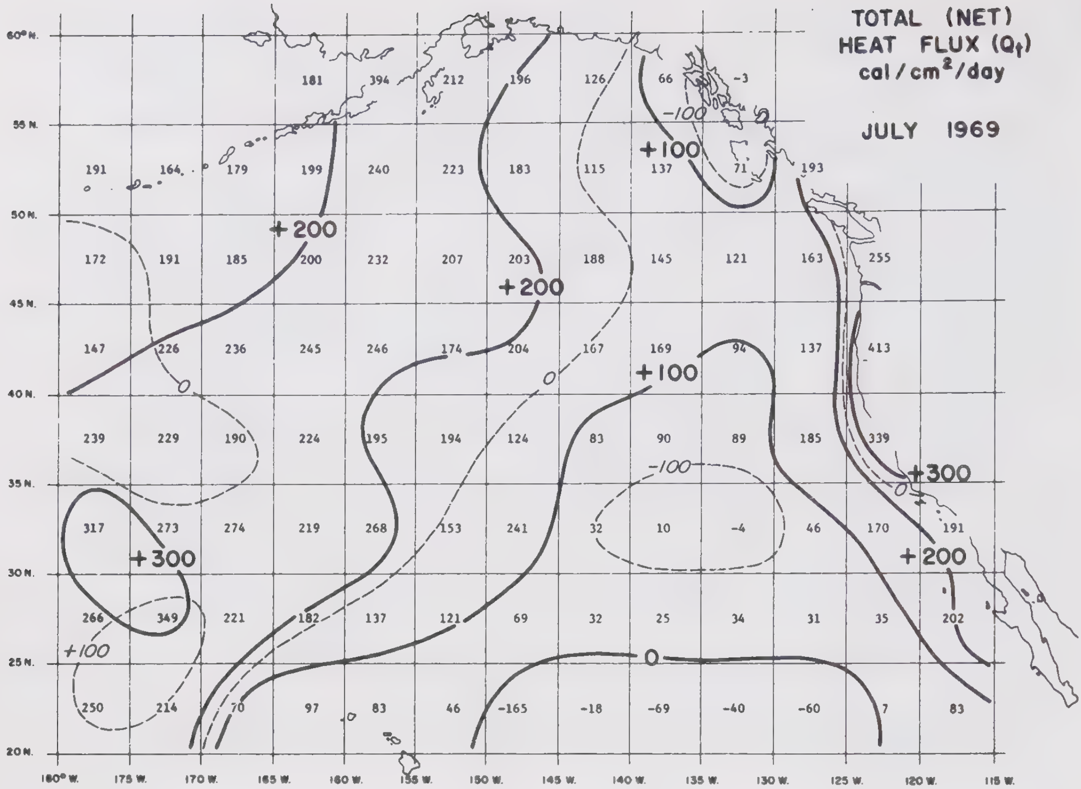
MAY 1969

60°N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W
165 W.
160 W.
155 W.
150 W.
145 W
140 W
135 W
130 W
125 W.
120 W.
115 W
133 151 260 139 87 77 164
196 167 209 198 283 202 195 192 254 278
226 214 226 218 223 185 227 195 252 221 237 212
107 130 149 138 143 144 171 173 249 229 201 211
231 188 105 145 145 96 145 138 201 204 275 276
146 128 178 173 80 103 165 120 167 204 251 254 140
168 142 119 53 78 158 142 139 137 211 127 35 120
174 43 103 77 111 176 168 98 -12 24 67 46 58
+200
+100
0
-100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JUNE 1969

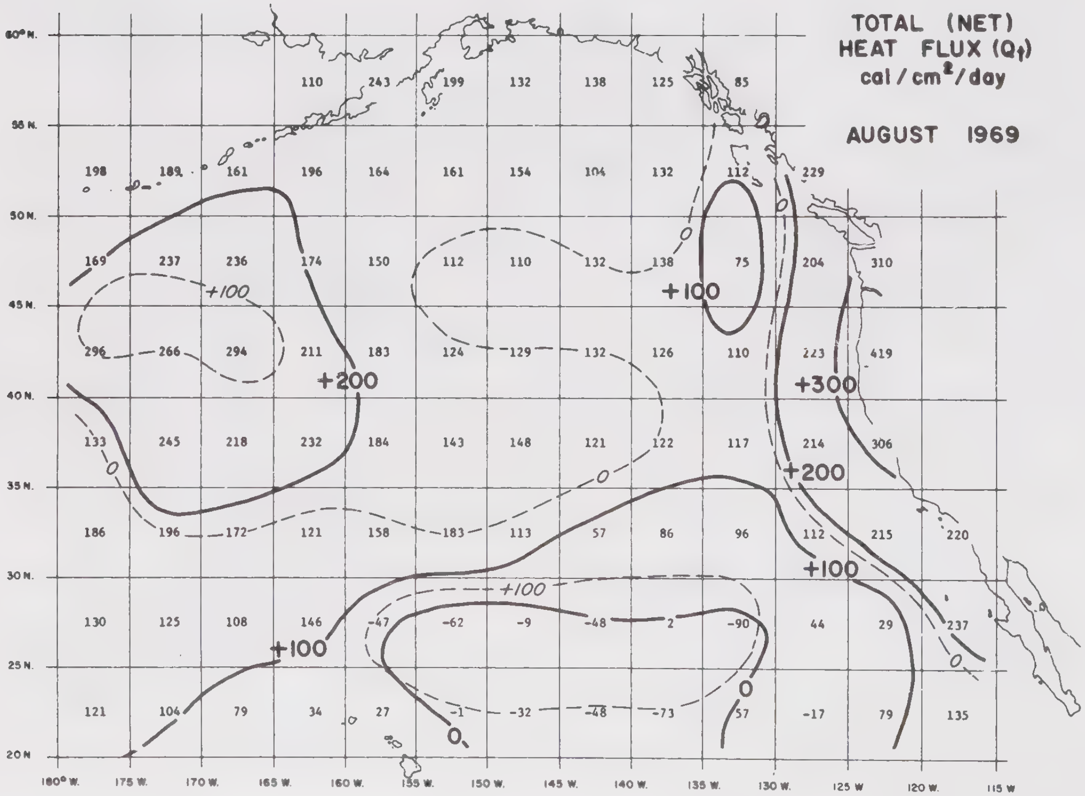
60°N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N
25 N
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W
125 W.
120 W.
115 W
202 205 254 226 159 159 410
183 184 212 220 207 192 211 197 198 218 363
206 218 250 227 226 281 209 197 208 194 249 169
181 184 143 122 234 210 246 273 214 199 173 208
152 134 189 159 245 247 249 202 236 192 185 287
124 147 147 223 252 215 230 194 203 198 169 248 244
143 190 152 185 240 159 177 131 148 125 99 147 189
255 35 178 215 206 154 123 128 53 106 92 144 106
+200
+100
0
-100



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

JULY 1969

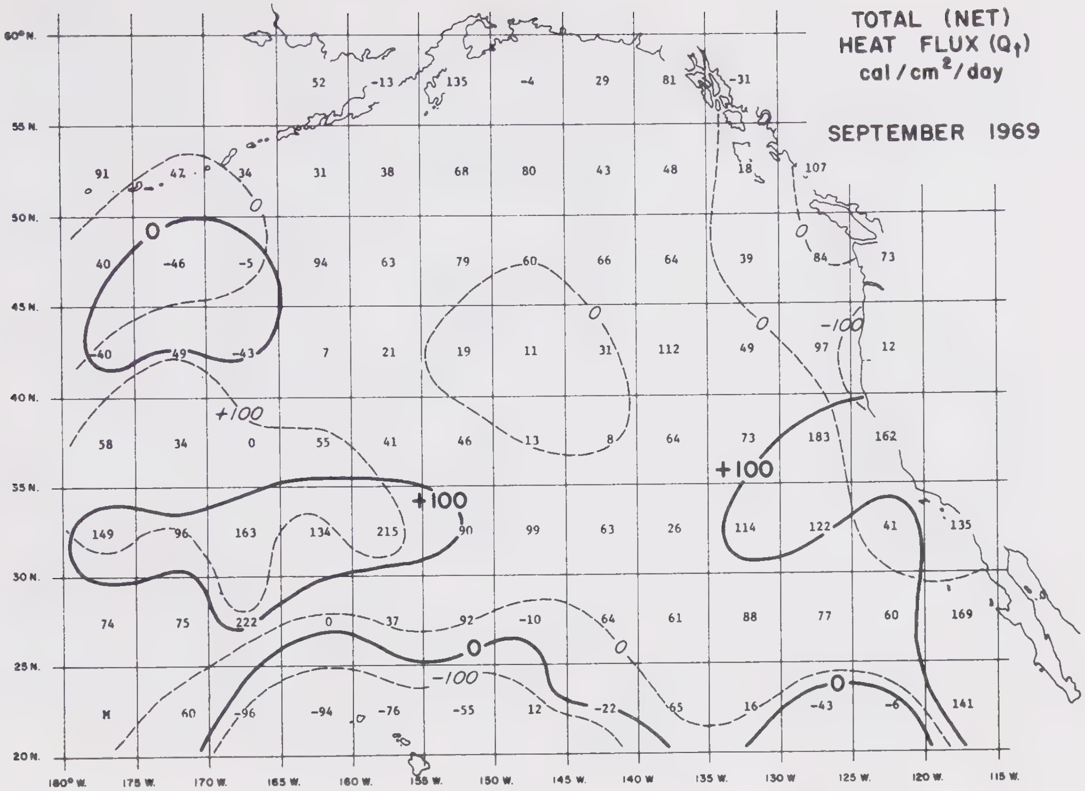
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
181 394 212 196 126 66 -3
191 164 179 199 240 223 183 115 137 71 193
172 191 185 200 232 207 203 188 145 121 163 255
147 226 236 245 246 174 204 167 169 94 137 413
239 229 190 224 195 194 124 83 90 89 185 339
317 273 274 219 268 153 241 32 10 -4 46 170 191
266 349 221 182 137 121 69 32 25 34 31 35 202
250 214 70 97 83 46 -165 -18 -69 -40 -60 7 83
-100
+100
+200
+200
+100
0
-100
+300
+300
+200
+100
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

AUGUST 1969

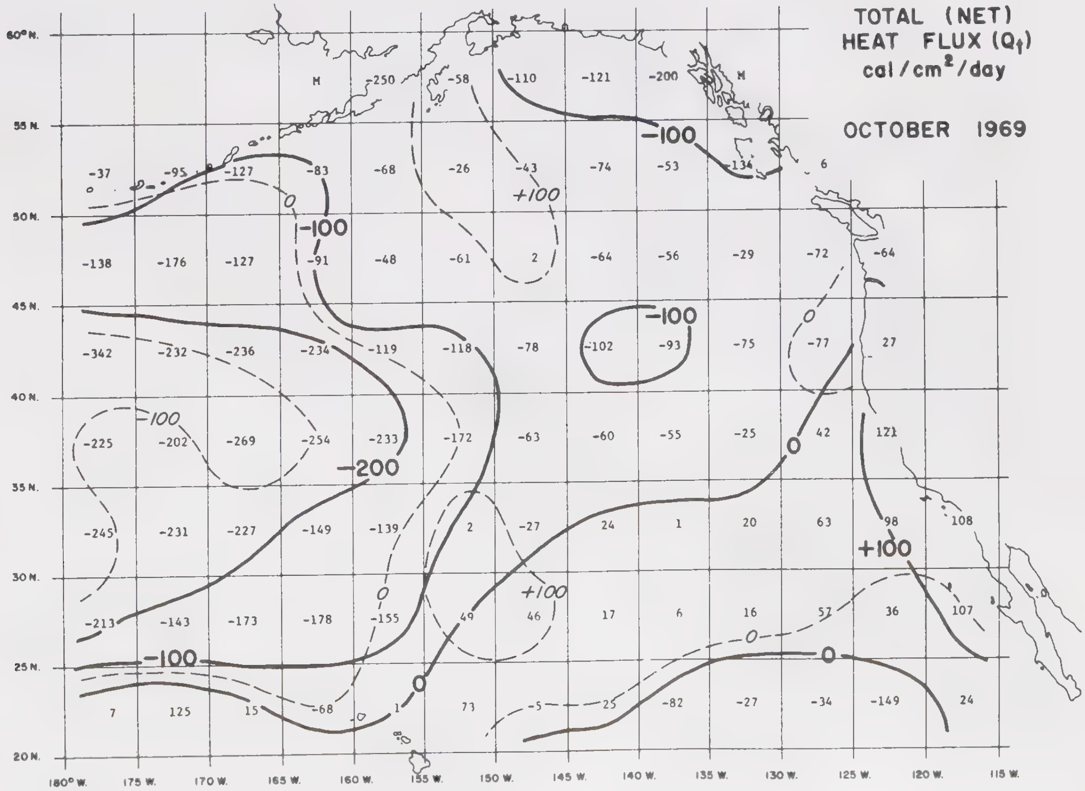
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W
120 W.
115 W
110 243 199 132 138 125 85
198 189 161 196 164 161 154 104 132 112 229
169 237 236 174 150 112 110 132 138 75 204 310
296 266 294 211 183 124 129 132 126 110 223 419
133 245 218 232 184 143 148 121 122 117 214 306
186 196 172 121 158 183 113 57 86 96 112 215 220
130 125 108 146 -47 -62 -9 -48 2 -90 44 29 237
121 104 79 34 27 -1 -32 -48 -73 57 -17 79 135
+100
+200
0
+100
0
+300
+200
+100
+100
+100
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

SEPTEMBER 1969

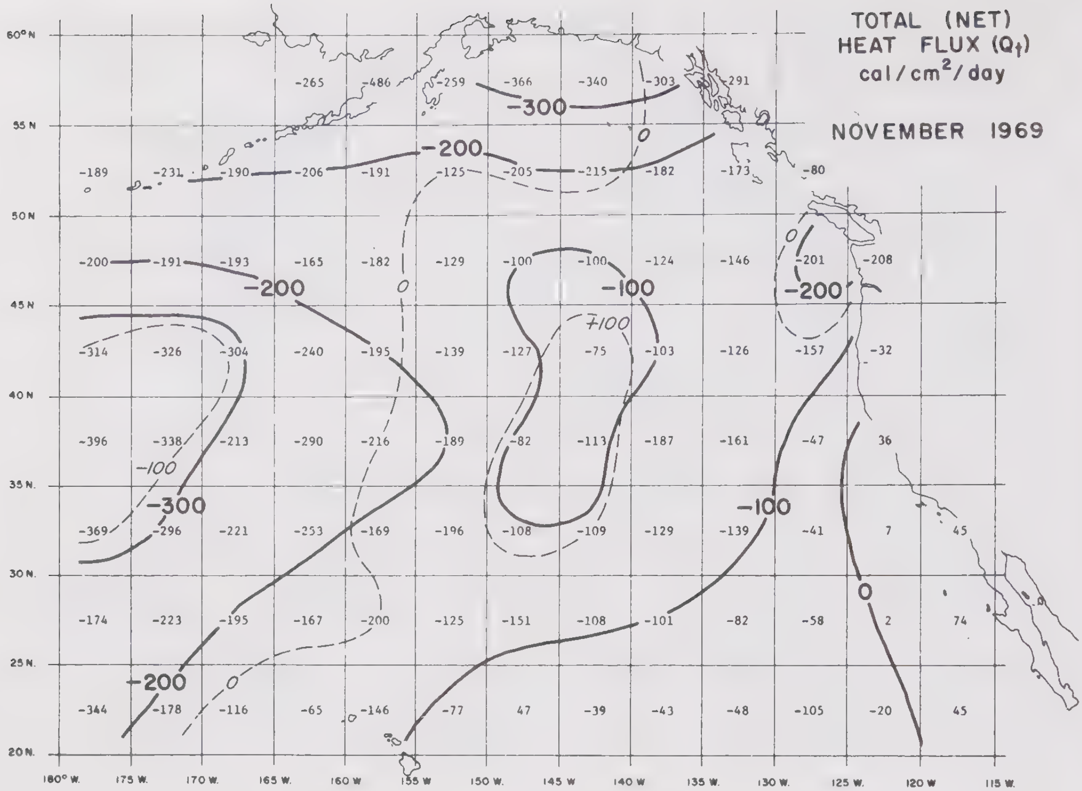
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W
135 W.
130 W
125 W.
120 W.
115 W.
0
+100
-100



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

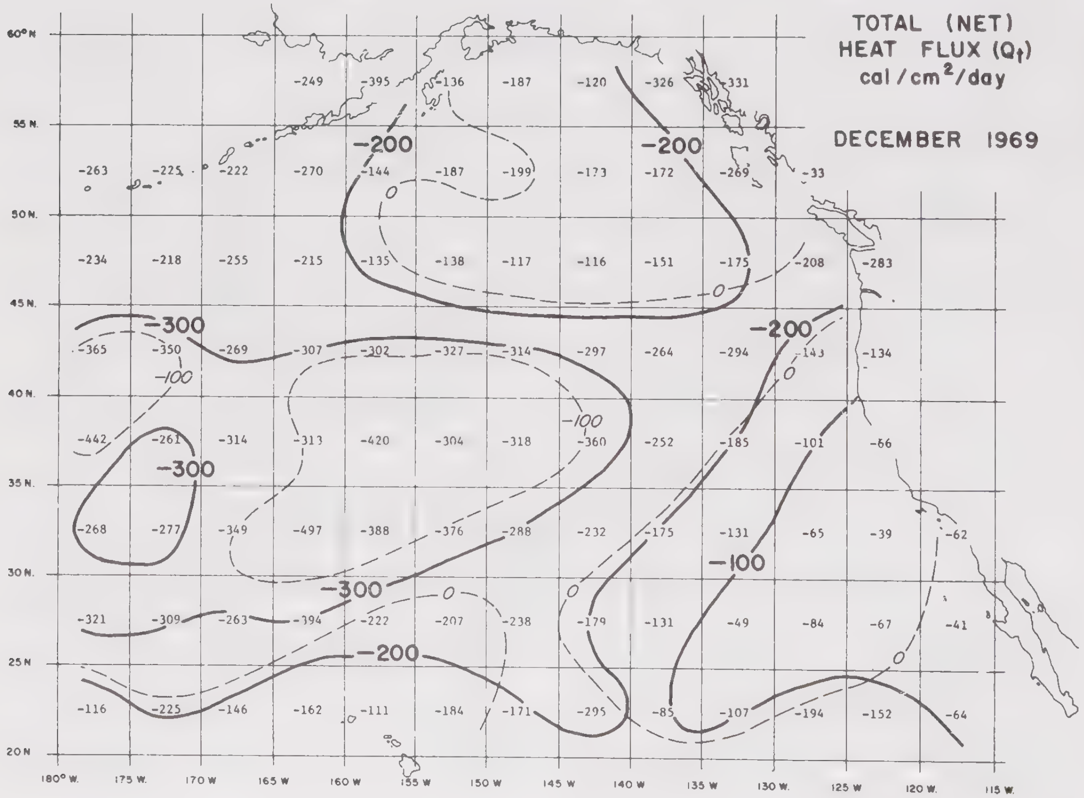
OCTOBER 1969

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
0
-100
-200
+100


TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

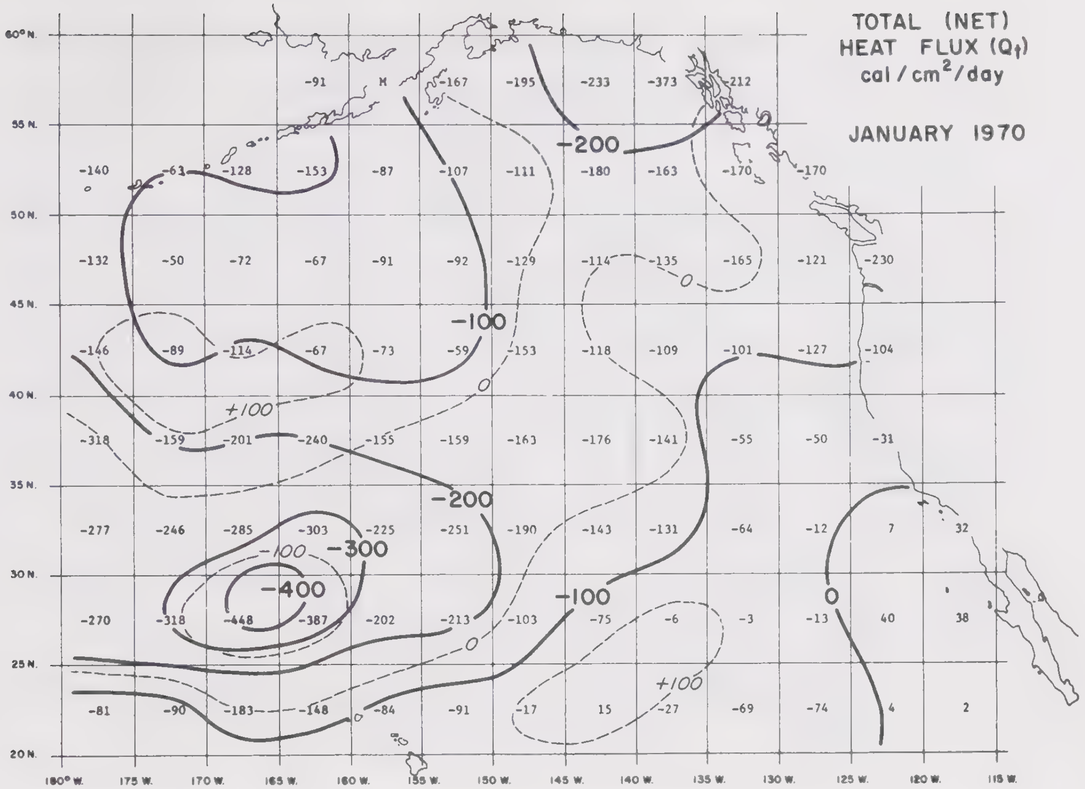
NOVEMBER 1969

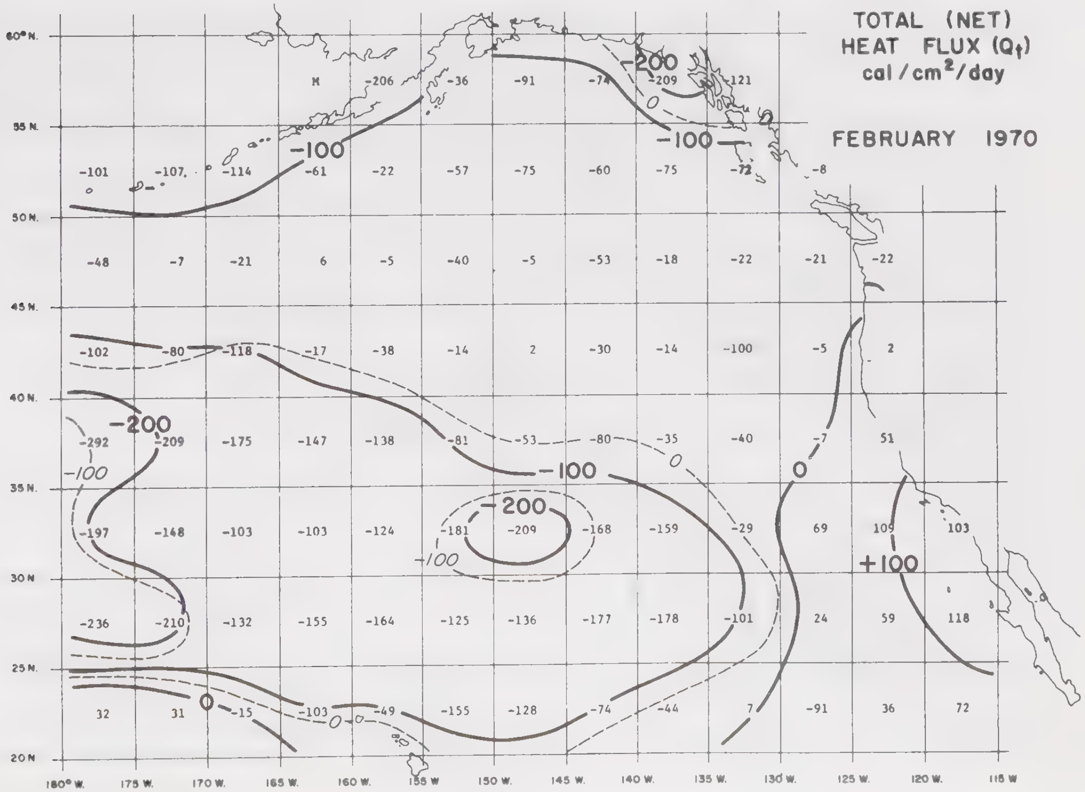
60°N
55 N
50 N
45 N
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W
155 W
150 W.
145 W
140 W
135 W.
130 W.
125 W.
120 W
115 W.
-265 -486 -259 -366 -340 -303 -291
-300
0
-200
-189 -231 -190 -206 -191 -125 -205 -215 -182 -173 -80
-200 -191 -193 -165 -182 -129 -100 -100 -124 -146 -201 -208
0
-200
-100
-200
+100
-314 -326 -304 -240 -195 -139 -127 -75 -103 -126 -157 -32
-396 -338 -213 -290 -216 -189 -82 -113 -187 -161 -47 36
-100
-300
-100
-369 -296 -221 -253 -169 -196 -108 -109 -129 -139 -41 7 45
0
-174 -223 -195 -167 -200 -125 -151 -108 -101 -82 -58 2 74
-200
0
-344 -178 -116 -65 -146 -77 47 -39 -43 -48 -105 -20 45

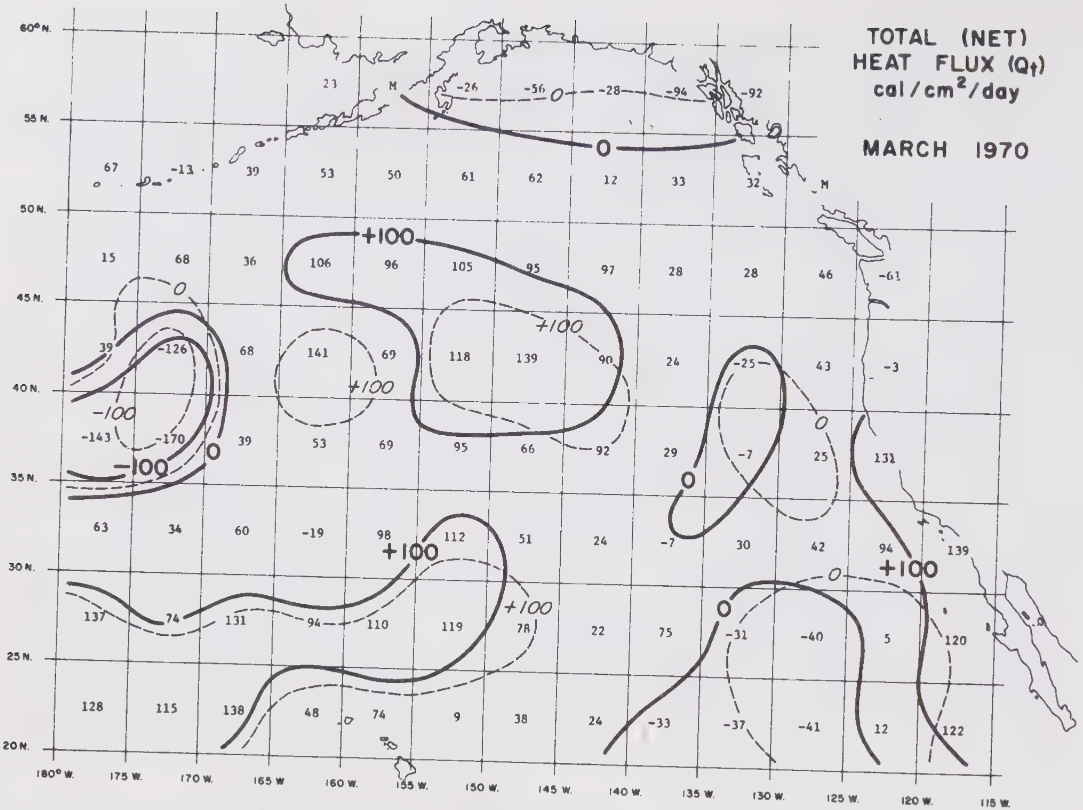

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

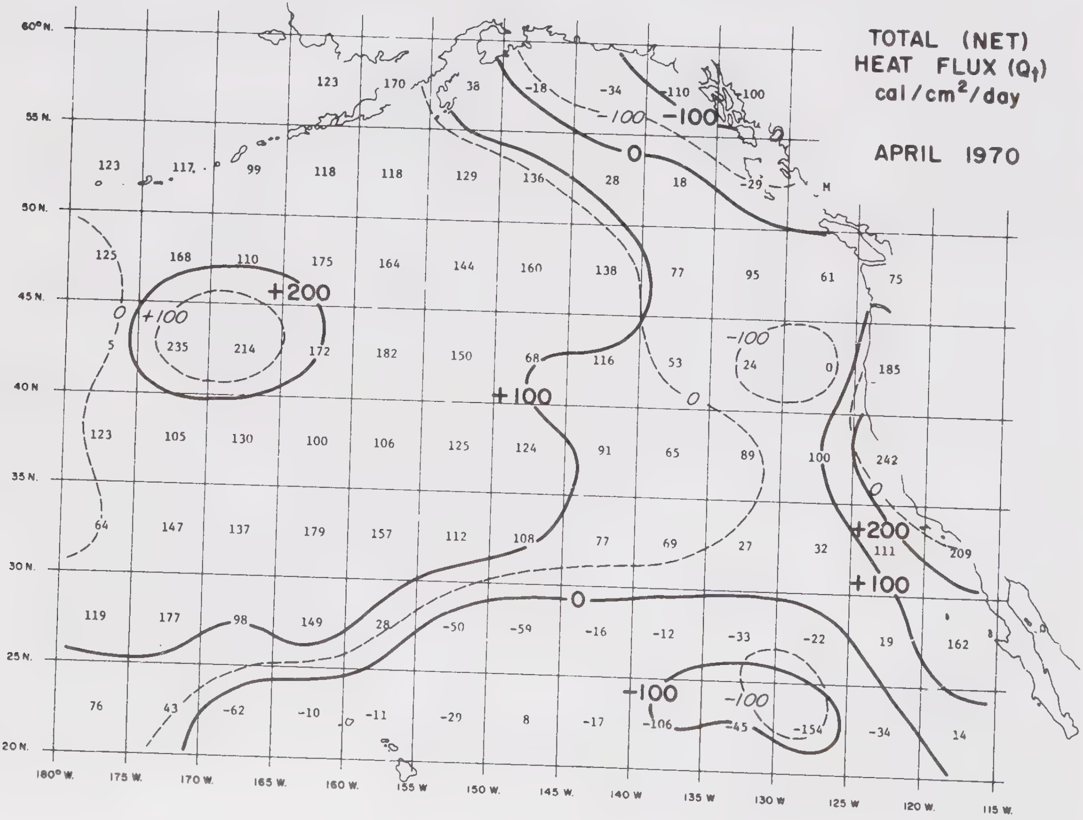
DECEMBER 1969

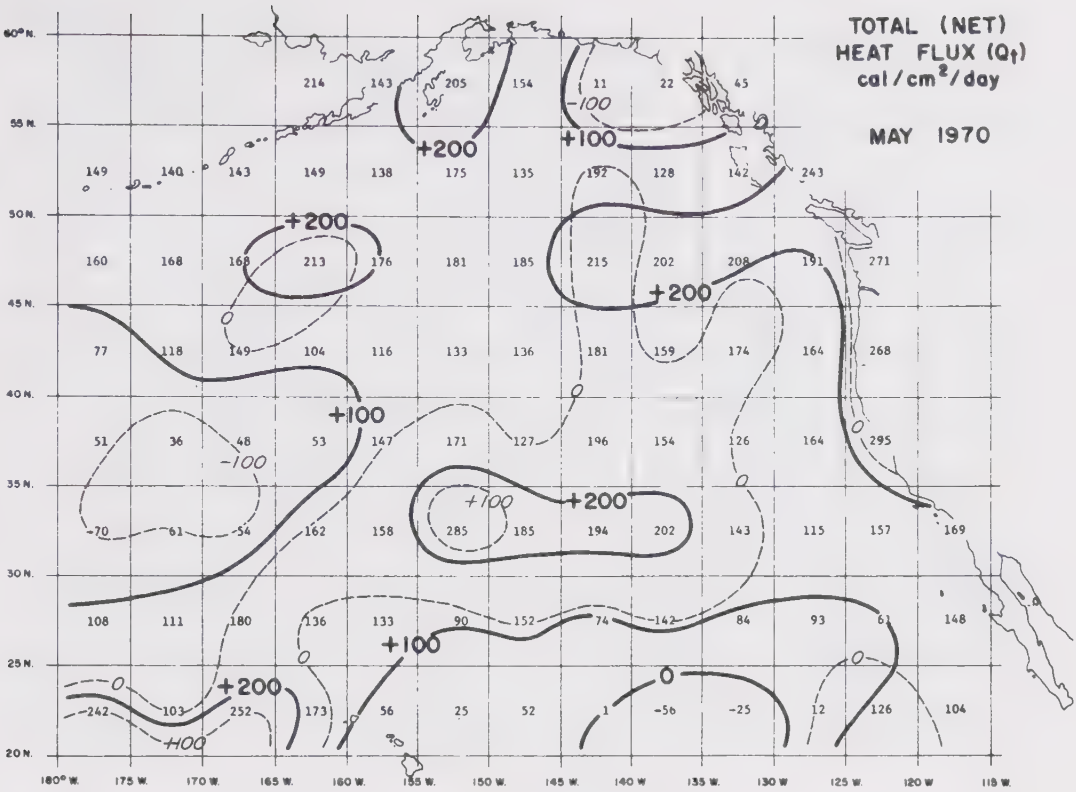
60°N
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N
20 N
180° W.
175 W.
170 W
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W.
125 W
120 W.
115 W.
-249 -395 -136 -187 -120 -326 -331
-200
-200
-263 -225 -222 -270 -144 -187 -199 -173 -172 -269 -33
0
-234 -218 -255 -215 -135 -138 -117 -116 -151 -175 -208 -283
0
-300
-200
-365 -350 -269 -307 -302 -327 -314 -297 -264 -294 -143 -134
-100
0
-100
-442 -261 -314 -313 -420 -304 -318 -360 -252 -185 -101 -66
-300
-268 -277 -349 -497 -388 -376 -288 -232 -175 -131 -65 -39 -62
-100
-300
0
0
-321 -309 -263 -394 -222 -207 -238 -179 -131 -49 -84 -67 -41
-200
0
-116 -225 -146 -162 -111 -184 -171 -295 -85 -107 -194 -152 -64

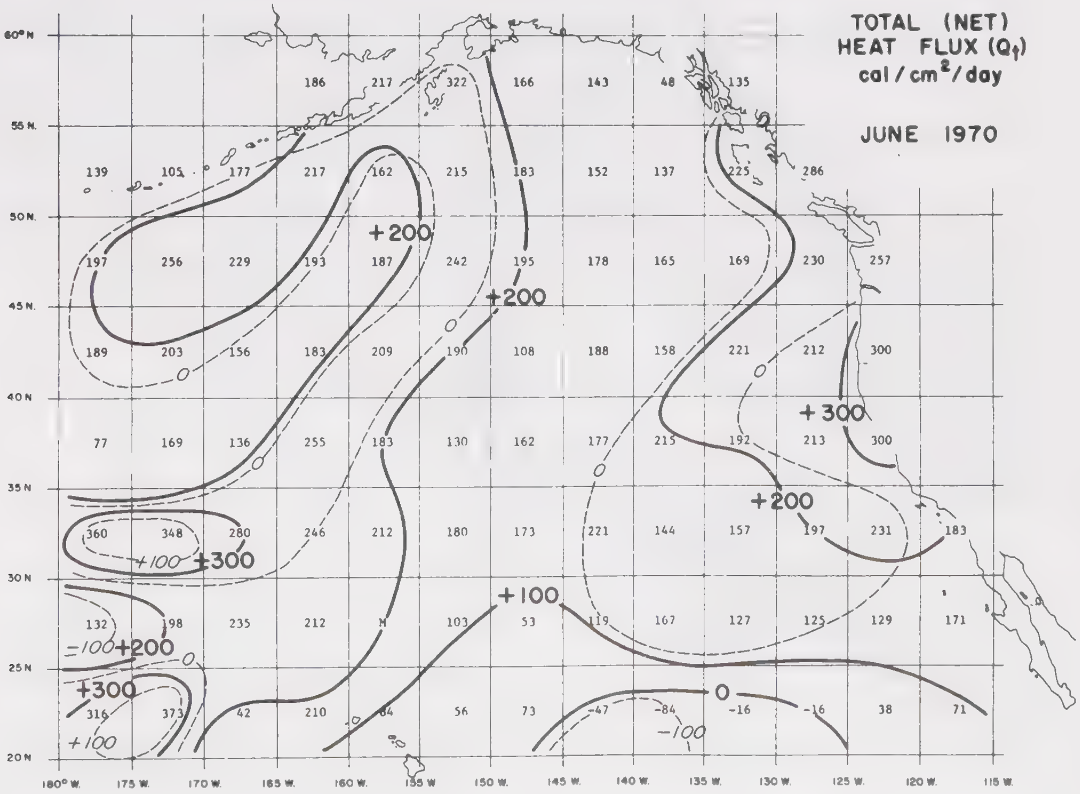

TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm² / day
JANUARY 1970
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-91
M
-167
-195
-233
-373
-212
-200
-140
-63
-128
-153
-87
-107
-111
-180
-163
-170
-170
-132
-50
-72
-67
-91
-92
-129
-114
-135
0
-165
-121
-230
-100
-146
-89
-114
-67
-73
-59
-153
-118
-109
-101
-127
-104
0
+100
-318
-159
-201
-240
-155
-159
-163
-176
-141
-55
-50
-31
-200
-277
-246
-285
-303
-225
-251
-190
-143
-131
-64
-12
7
32
-100
-300
-400
-100
0
-270
-318
-448
-387
-202
-213
-103
-75
-6
-3
-13
40
38
0
+100
-81
-90
-183
-148
0
-84
-91
-17
15
-27
-69
-74
4
2

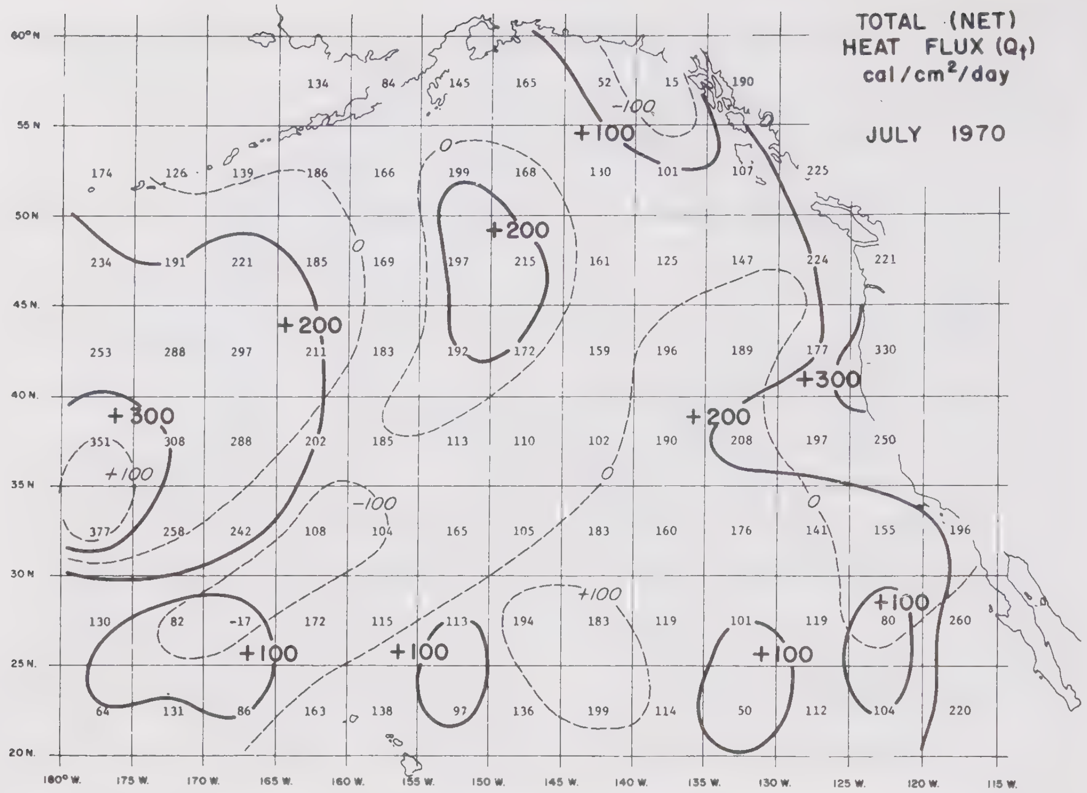

TOTAL (NET)
HEAT FLUX (Q_t)
cal / cm² / day
FEBRUARY 1970
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-200
M
-206
-36
-91
-74
-209
0
-121
-100
-100
-101
-107
-114
-61
-22
-57
-75
-60
-75
-72
-8
-48
-7
-21
6
-5
-40
-5
-53
-18
-22
-21
-22
-102
-80
-118
-17
-38
-14
2
-30
-14
-100
-5
2
-200
-292
-209
-175
-147
-138
-81
-53
-80
-35
0
-40
-7
51
-100
-100
0
-200
-197
-148
-103
-103
-124
-181
-209
-168
-159
-29
69
109
103
-100
+100
-236
-210
-132
-155
-164
-125
-136
-177
-178
-101
24
59
118
0
32
31
-15
-103
0
-49
-155
-128
-74
-44
7
-91
36
72

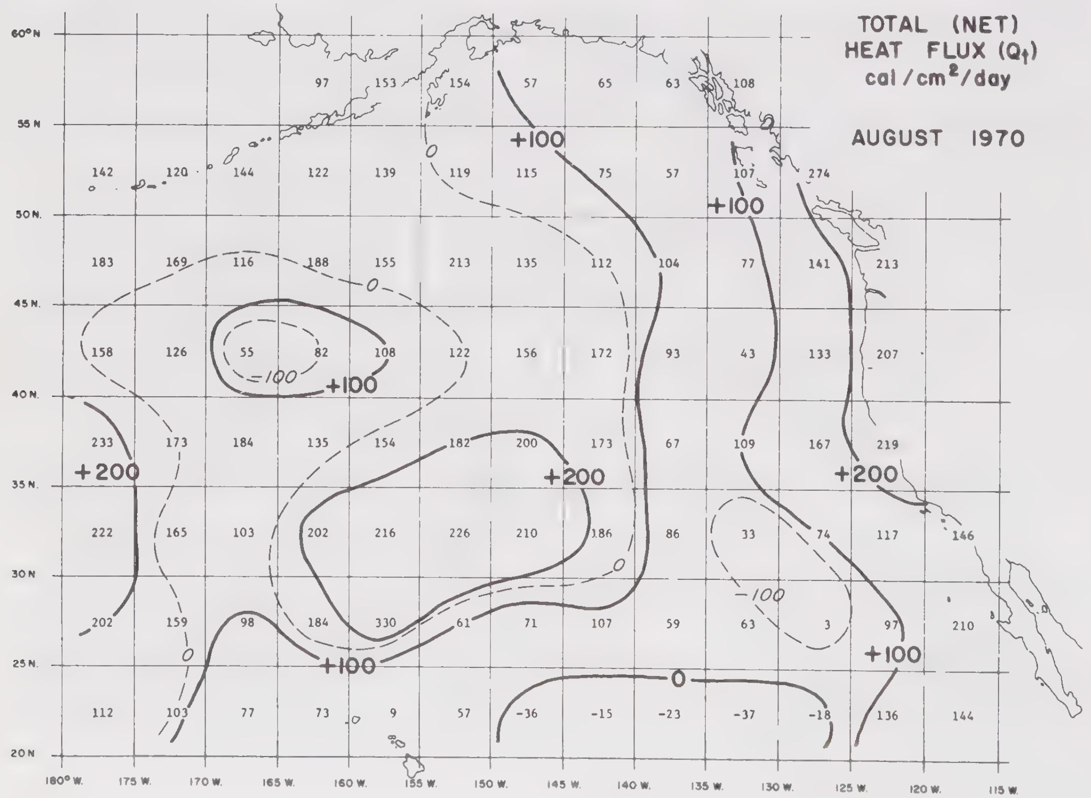

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
MARCH 1970
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
23
M
-26
-56
0
-28
-94
-92
0
67
-13
39
53
50
61
62
12
33
32
M
+100
15
68
36
106
96
105
95
97
28
28
46
-61
0
39
-126
68
141
69
118
+100
139
90
24
-25
43
-3
-100
+100
-143
-170
39
53
69
95
66
92
29
-7
0
25
131
-100
0
0
63
34
60
-19
98
112
+100
51
24
-7
30
42
94
+100
139
137
74
131
94
110
119
+100
78
22
75
0
-31
-40
5
120
128
115
138
48
74
9
38
24
-33
-37
-41
12
122

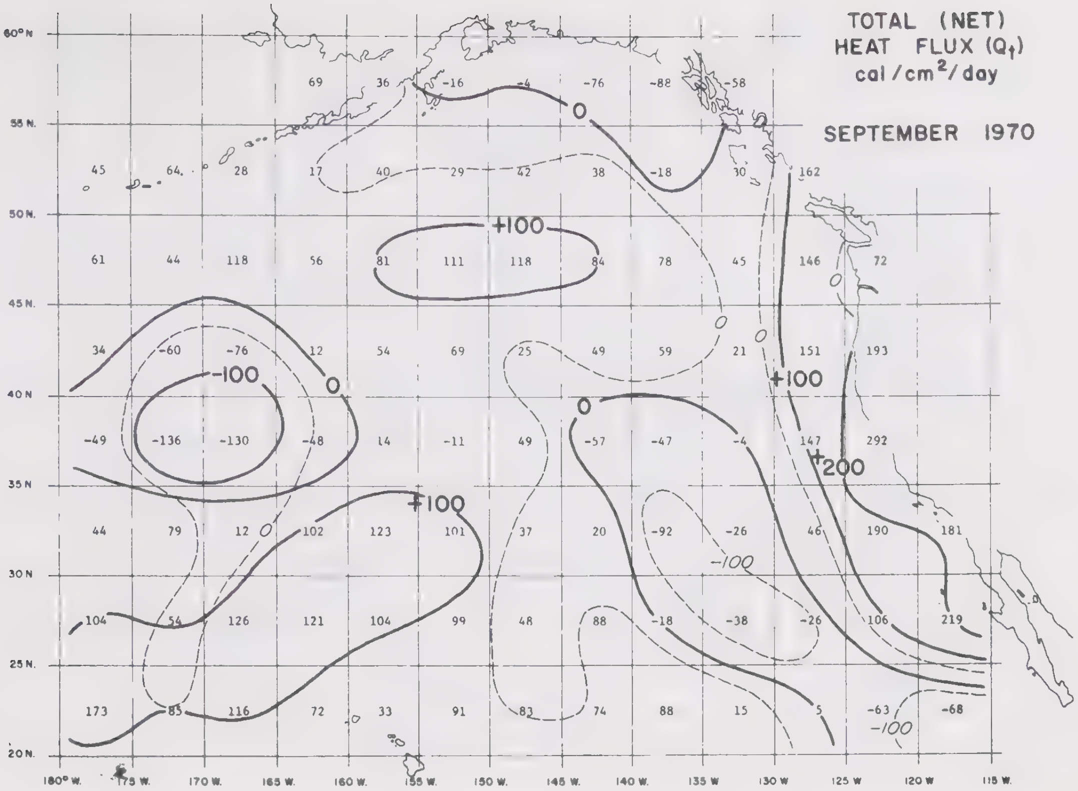

TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day
APRIL 1970
60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W.
145 W.
140 W
135 W
130 W
125 W
120 W.
115 W.
123
170
38
-18
-34
-110
-100
-100
-100
0
123
117
99
118
118
129
136
28
18
-29
M
125
168
110
175
164
144
160
138
77
95
61
75
+200
0
+100
5
235
214
172
182
150
68
116
53
-100
24
0
185
+100
0
123
105
130
100
106
125
124
91
65
89
100
242
0
64
147
137
179
157
112
108
77
69
27
32
+200
111
209
+100
119
177
98
149
28
-50
-59
0
-16
-12
-33
-22
19
162
76
43
-62
-10
-11
-29
8
-17
-100
-106
-100
-45
-154
-34
14


TOTAL (NET) HEAT FLUX (Q$_t$) cal/cm^2/day
MAY 1970
214 143 205 154 11 22 45
149 140 143 149 138 175 135 192 128 142 243
160 168 168 213 176 181 185 215 202 208 191 271
77 118 149 104 116 133 136 181 159 174 164 268
51 36 48 53 147 171 127 196 154 126 164 295
-70 -61 -54 162 158 285 185 194 202 143 115 157 169
108 111 180 136 133 90 152 74 -142 84 93 61 148
-242 -103 252 173 56 25 52 1 -56 -25 12 126 104
+200
+100
-100
0
+100
60°N. 55 N. 50 N. 45 N. 40 N. 35 N. 30 N. 25 N. 20 N.
180° W. 175 W. 170 W. 165 W. 160 W. 155 W. 150 W. 145 W. 140 W 135 W. 130 W. 125 W. 120 W 115 W.


TOTAL (NET) HEAT FLUX (Q$_t$) cal/cm^2/day
JUNE 1970
186 217 322 166 143 48 135
139 105 177 217 162 215 183 152 137 225 286
197 256 229 193 187 242 195 178 165 169 230 257
189 203 156 183 209 190 108 188 158 221 212 300
77 169 136 255 183 130 162 177 215 192 213 300
360 348 280 246 212 180 173 221 144 157 197 231 183
132 198 235 212 M 103 53 119 167 127 125 129 171
316 373 42 210 84 56 73 -47 -84 -16 -16 38 71
+200
+300
+100
-100
0
60°N 55 N. 50 N. 45 N. 40 N 35 N 30 N 25 N 20 N
180° W. 175 W. 170 W. 165 W. 160 W. 155 W 150 W. 145 W. 140 W. 135 W. 130 W. 125 W. 120 W. 115 W.


TOTAL (NET) HEAT FLUX (Q$_t$) cal/cm^2/day
JULY 1970
60°N
55 N
50 N
45 N.
40 N.
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
134 84 145 165 52 15 190
-100
+100
174 126 139 186 166 199 168 130 101 107 225
0
+200
234 191 221 185 169 197 215 161 125 147 224 221
+200
253 288 297 211 183 192 172 159 196 189 177 330
+300
+300
+200
351 308 288 202 185 113 110 102 190 208 197 250
+100
0
-100
0
377 258 242 108 104 165 105 183 160 176 141 155 196
+100
+100
130 82 -17 172 115 113 194 183 119 101 119 80 260
+100
+100
+100
64 131 86 163 138 97 136 199 114 50 112 104 220

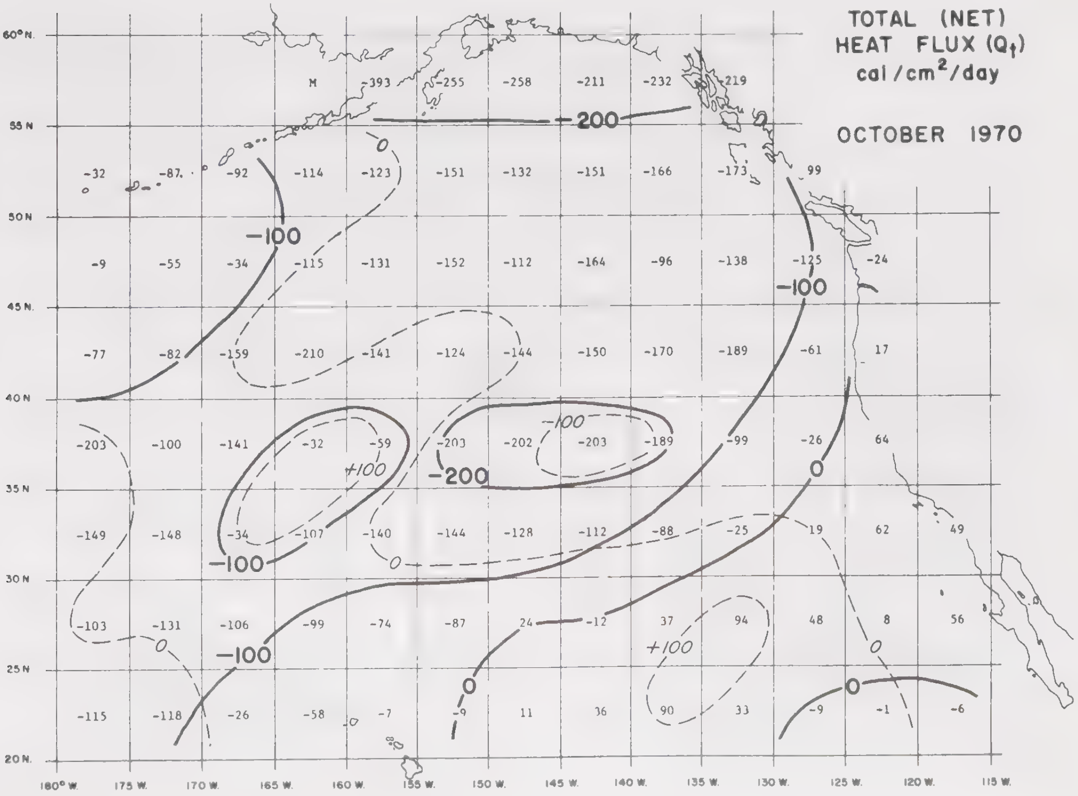

TOTAL (NET) HEAT FLUX (Q$_t$) cal/cm^2/day
AUGUST 1970
60°N
55 N
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
97 153 154 57 65 63 108
+100
0
142 120 144 122 139 119 115 75 57 107 274
+100
183 169 116 188 155 213 135 112 104 77 141 213
0
158 126 55 82 108 122 156 172 93 43 133 207
-100
+100
233 173 184 135 154 182 200 173 67 109 167 219
+200
+200
+200
222 165 103 202 216 226 210 186 86 33 74 117 146
0
-100
202 159 98 184 330 61 71 107 59 63 3 97 210
0
+100
+100
0
112 103 77 73 9 57 -36 -15 -23 -37 -18 136 144



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

SEPTEMBER 1970

60° N
55 N.
50 N.
45 N.
40 N
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W
130 W
125 W
120 W
115 W.
69 36 -16 -4 -76 -88 -58
45 64 28 17 40 29 42 38 -18 30 162
61 44 118 56 81 111 118 84 78 45 146 72
34 -60 -76 12 54 69 25 49 59 21 151 193
-49 -136 -130 -48 14 -11 49 -57 -47 -4 147 292
44 79 12 102 123 101 37 20 -92 -26 46 190 181
104 54 126 121 104 99 48 88 -18 -38 -26 106 219
173 83 116 72 33 91 83 74 88 15 5 -63 -68
0
+100
-100
0
0
+100
+200
0
-100
-100
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

OCTOBER 1970

60° N.
55 N
50 N
45 N.
40 N
35 N
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -393 -255 -258 -211 -232 -219
-32 -87 -92 -114 -123 -151 -132 -151 -166 -173 99
-9 -55 -34 -115 -131 -152 -112 -164 -96 -138 -125 -24
-77 -82 -159 -210 -141 -124 -144 -150 -170 -189 -61 17
-203 -100 -141 -32 -59 -203 -202 -203 -189 -99 -26 64
-149 -148 -34 -107 -140 -144 -128 -112 -88 -25 19 62 49
-103 -131 -106 -99 -74 -87 24 -12 37 94 48 8 56
-115 -118 -26 -58 -7 -9 11 36 90 33 -9 -1 -6
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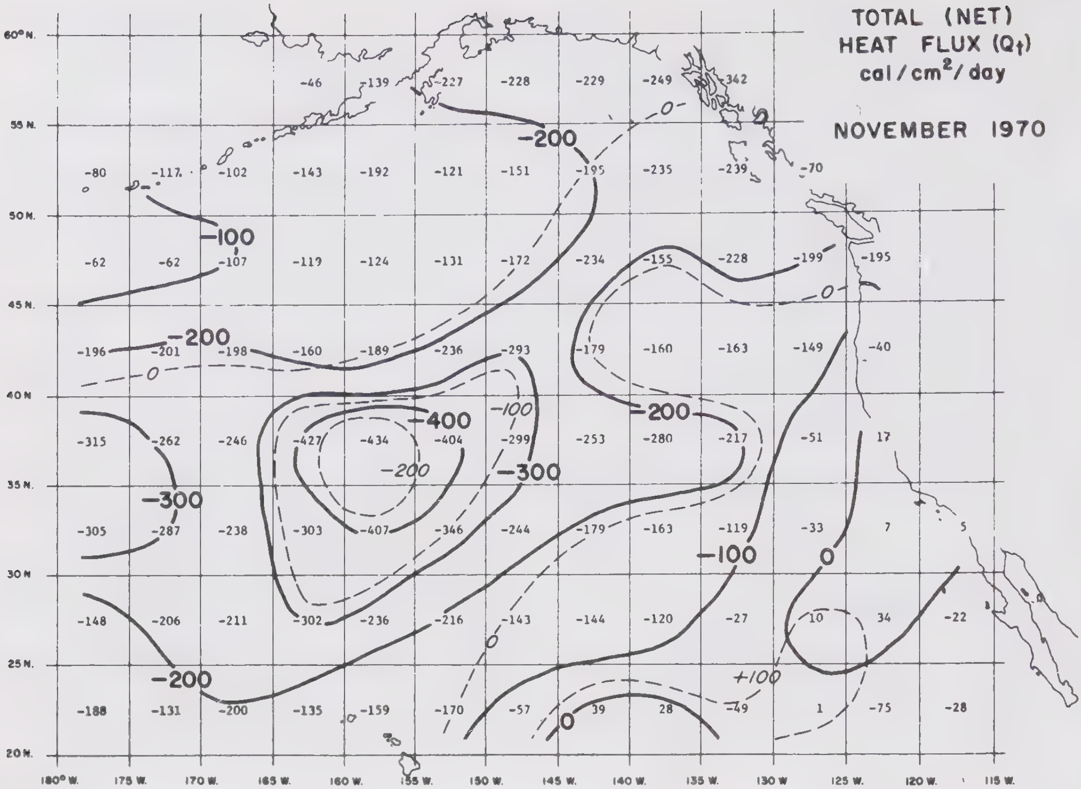
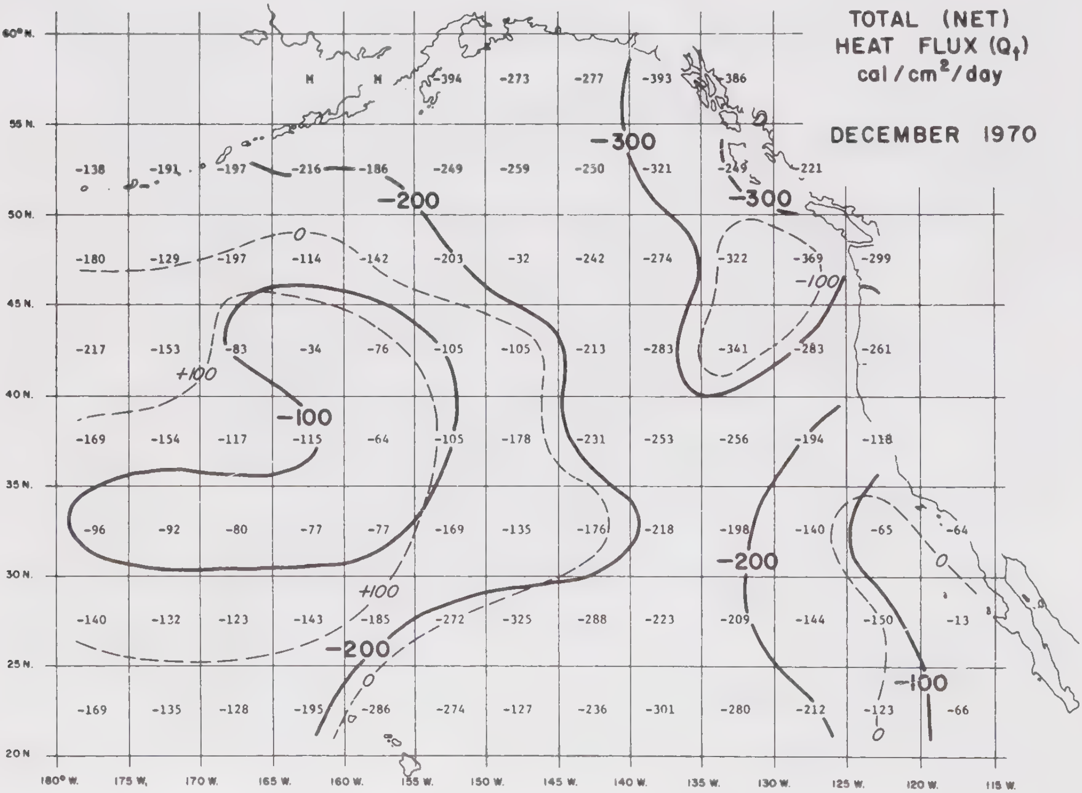
0
-100
-100
+100
-100
-200
-100
-100
0
0
+100
0
0
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

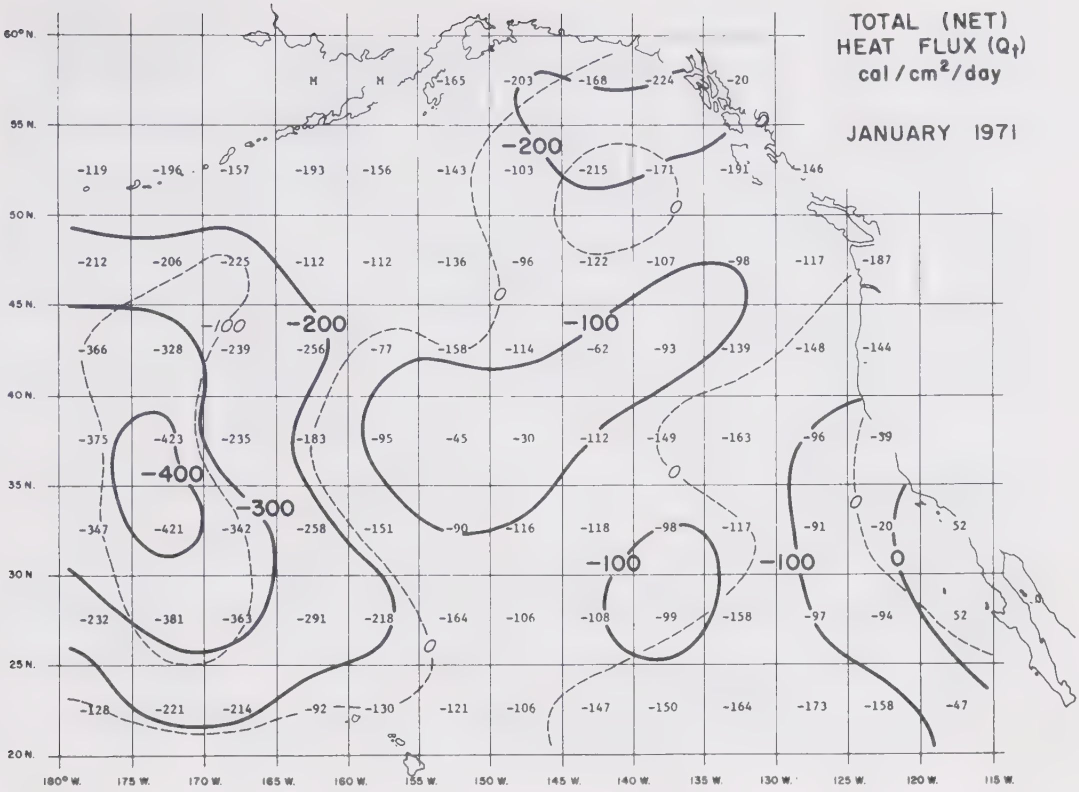
NOVEMBER 1970

60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W
125 W.
120 W.
115 W.
-46 -139 -227 -228 -229 -249 -342
-80 -117 -102 -143 -192 -121 -151 -195 -235 -239 -70
-62 -62 -107 -119 -124 -131 -172 -234 -155 -228 -199 -195
-196 -201 -198 -160 -189 -236 -293 -179 -160 -163 -149 -40
-315 -262 -246 -427 -434 -404 -299 -253 -280 -217 -51 17
-305 -287 -238 -303 -407 -346 -244 -179 -163 -119 -33 7 5
-148 -206 -211 -302 -236 -216 -143 -144 -120 -27 10 34 -22
-188 -131 -200 -135 -159 -170 -57 39 28 -49 1 -75 -28
-200
-100
-200
0
-400
-100
-200
-300
-300
-200
-300
-100
0
-200
+100
0
0


TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

DECEMBER 1970

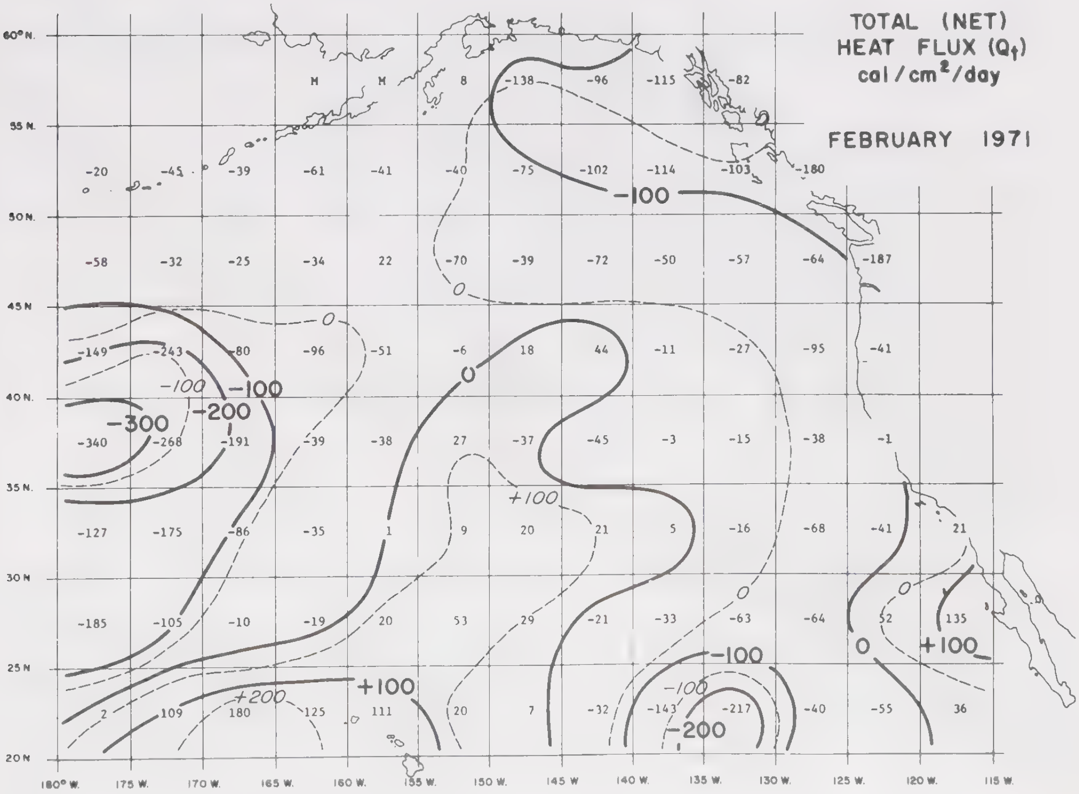
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M M -394 -273 -277 -393 -386
-138 -191 -197 -216 -186 -249 -259 -250 -321 -249 -221
-180 -129 -197 -114 -142 -203 -32 -242 -274 -322 -369 -299
-217 -153 -83 -34 -76 -105 -105 -213 -283 -341 -283 -261
-169 -154 -117 -115 -64 -105 -178 -231 -253 -256 -194 -118
-96 -92 -80 -77 -77 -169 -135 -176 -218 -198 -140 -65 -64
-140 -132 -123 -143 -185 -272 -325 -288 -223 -209 -144 -150 -13
-169 -135 -128 -195 -286 -274 -127 -236 -301 -280 -212 -123 -66
-300
-300
-200
0
-100
+100
-100
+100
-200
-200
0
-100
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

JANUARY 1971

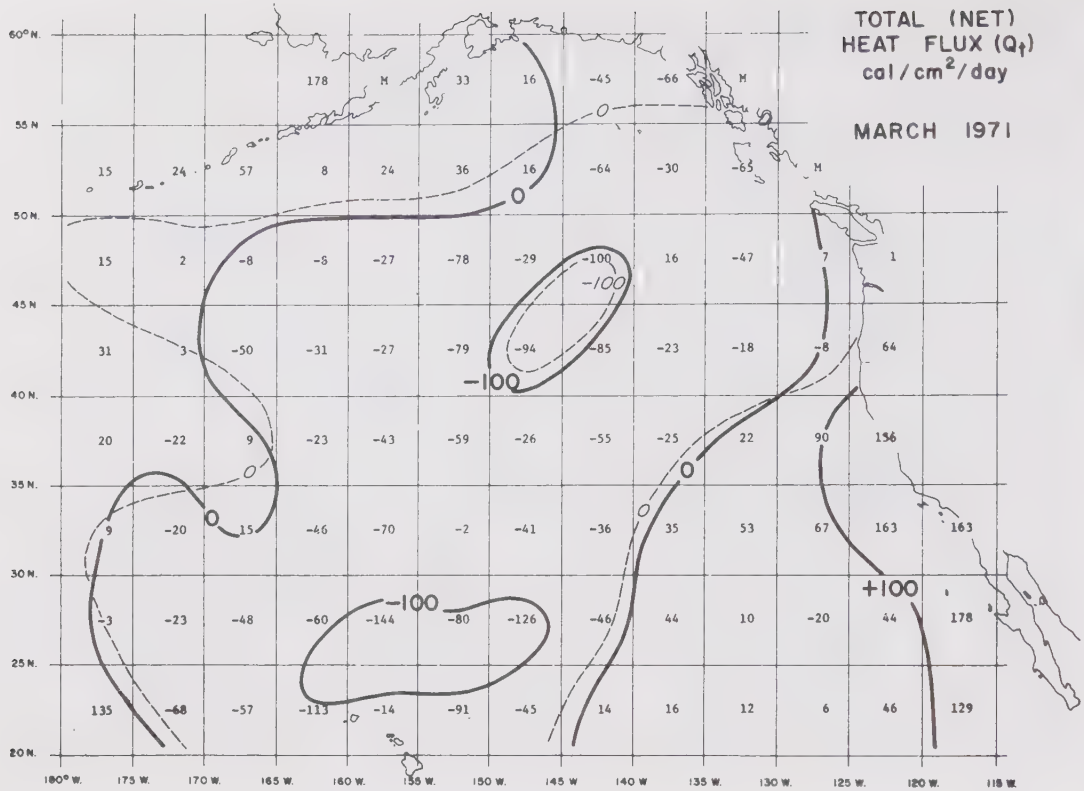
M M -165 -203 -168 -224 -20
-119 -196 -157 -193 -156 -143 -103 -215 -171 -191 -146
-212 -206 -225 -112 -112 -136 -96 -122 -107 -98 -117 -187
-366 -328 -239 -256 -77 -158 -114 -62 -93 -139 -148 -144
-375 -423 -235 -183 -95 -45 -30 -112 -149 -163 -96 -39
-347 -421 -342 -258 -151 -90 -116 -118 -98 -117 -91 -20 52
-232 -381 -363 -291 -218 -164 -106 -108 -99 -158 -97 -94 52
-128 -221 -214 -92 -130 -121 -106 -147 -150 -164 -173 -158 -47
-200
-200
-100
-100
-400
-300
0
-100
-100
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

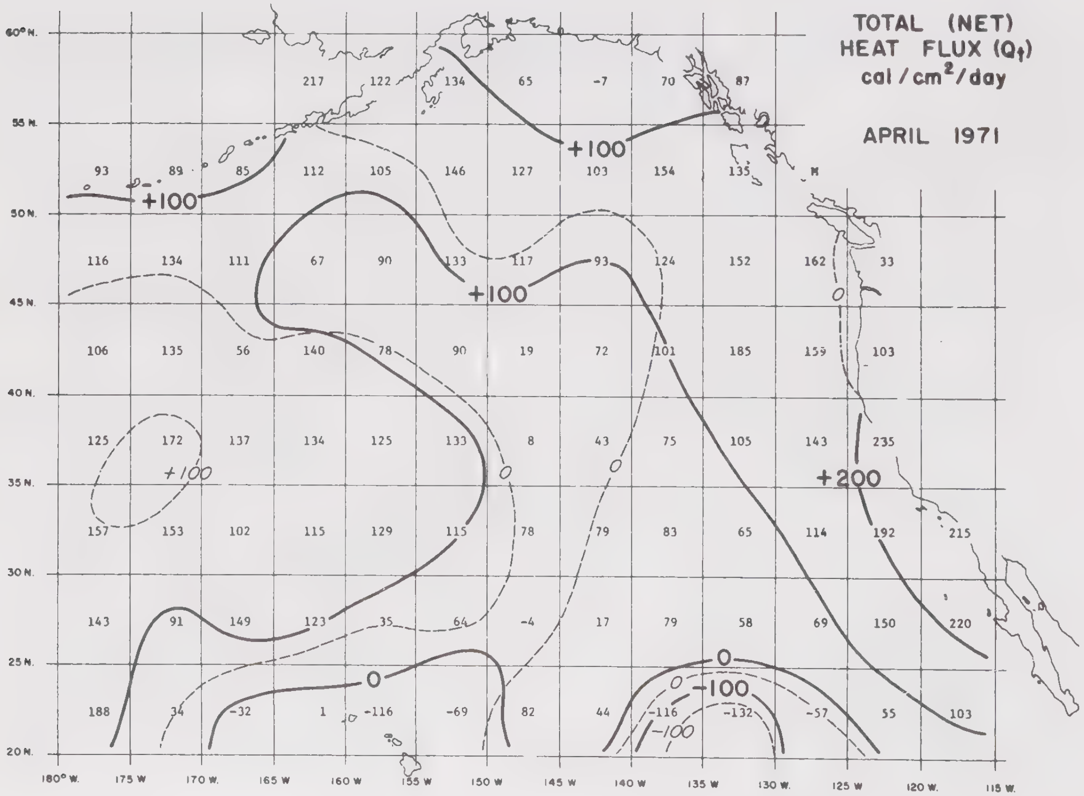


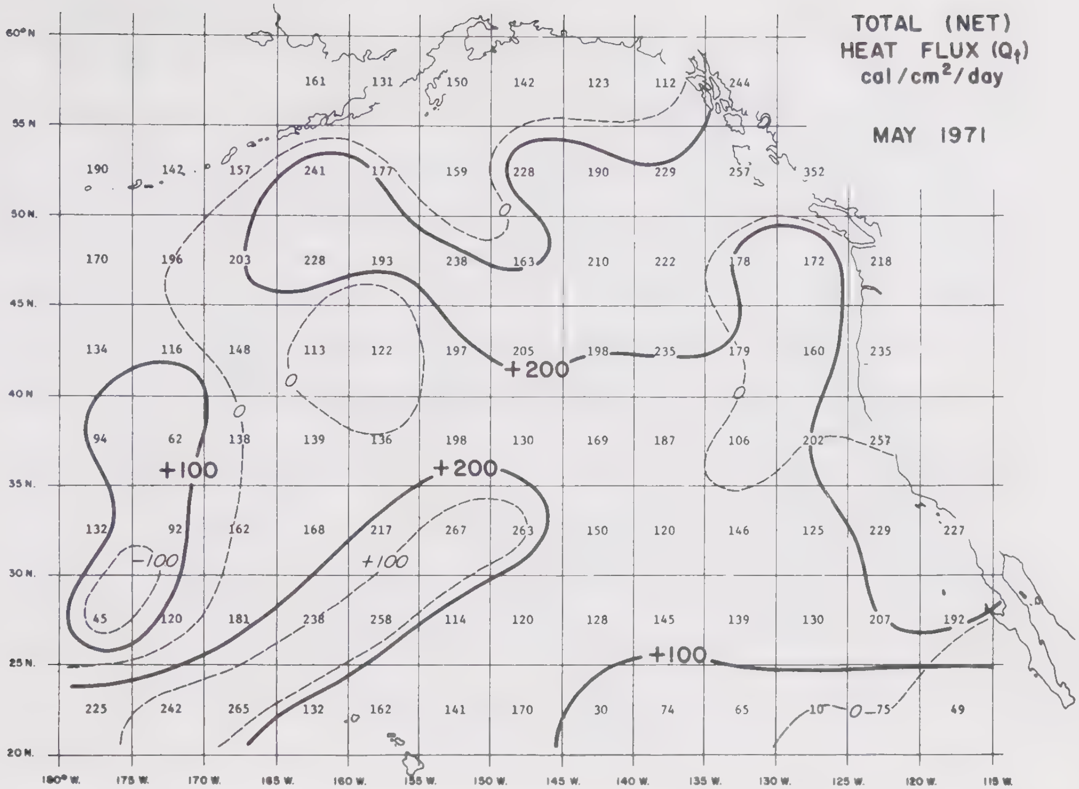
TOTAL (NET) HEAT FLUX (Q_t) cal/cm²/day

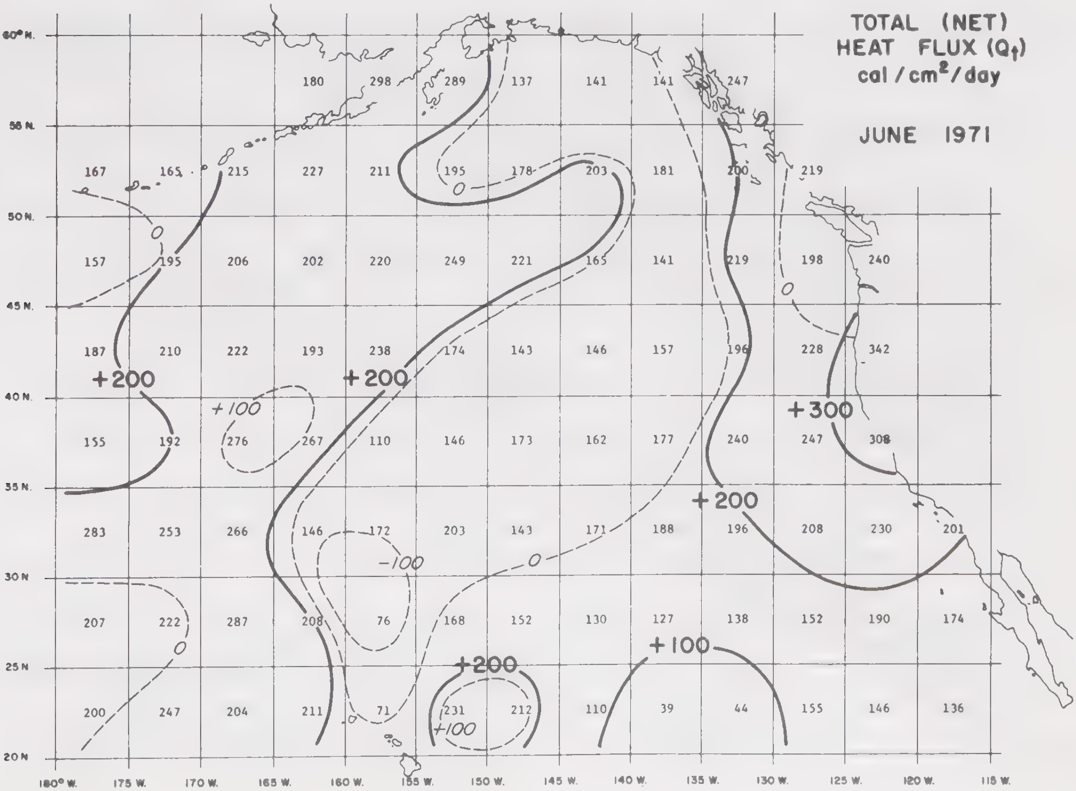
FEBRUARY 1971

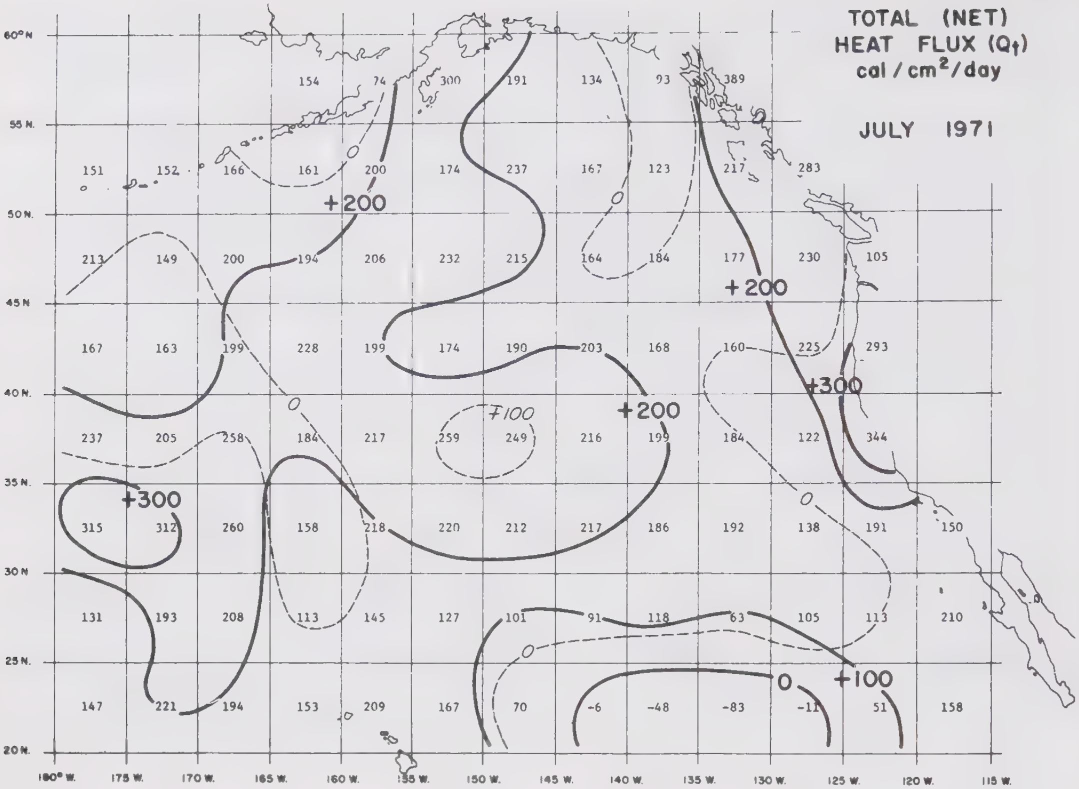
M M 8 -138 -96 -115 -82
-20 -45 -39 -61 -41 -40 -75 -102 -114 -103 -180
-58 -32 -25 -34 22 -70 -39 -72 -50 -57 -64 -187
-149 -243 -80 -96 -51 -6 18 44 -11 -27 -95 -41
-340 -268 -191 -39 -38 27 -37 -45 -3 -15 -38 -1
-127 -175 -86 -35 1 9 20 21 5 -16 -68 -41 21
-185 -105 -10 -19 20 53 29 -21 -33 -63 -64 52 135
2 -109 180 -125 111 20 7 -32 -143 -217 -40 -55 36
-100
0
0
-100
-100
-200
-300
+100
0
-100
0
+100
+100
+200
-100
-200
60° N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

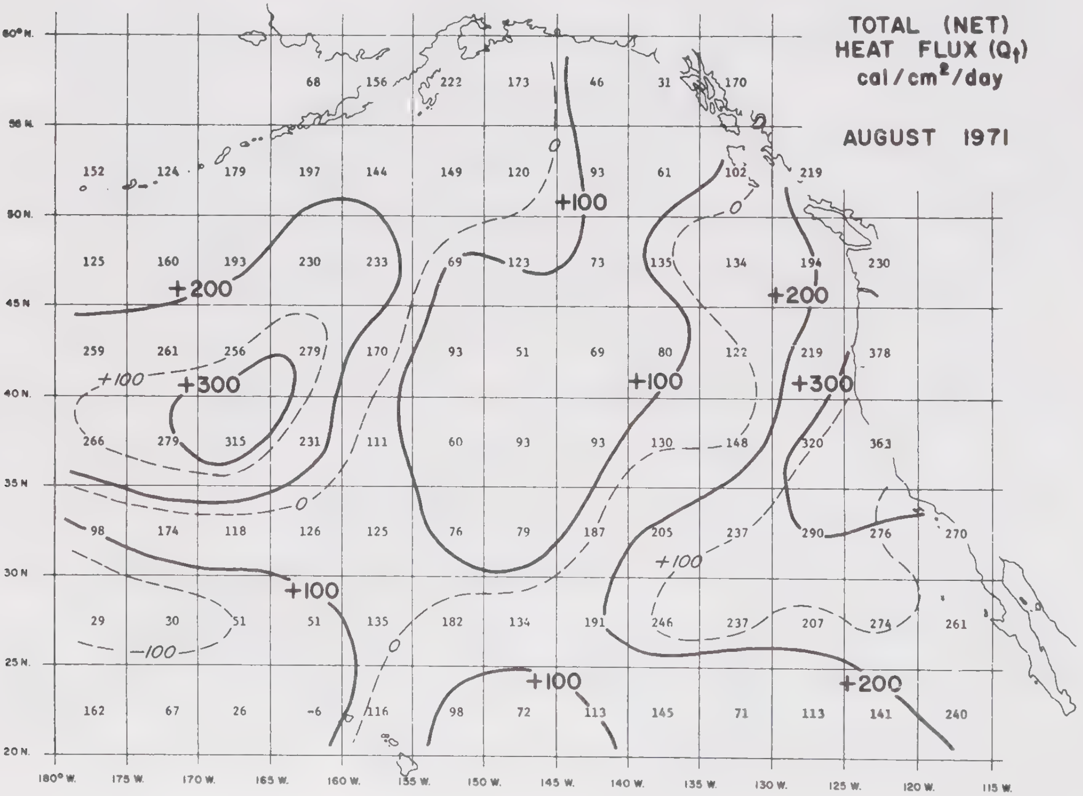

TOTAL (NET) HEAT FLUX (Q_t)
cal / cm²/ day
MARCH 1971
60° N.
55 N
50 N.
45 N
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W
140 W
135 W.
130 W.
125 W.
120 W.
115 W.
178 M 33 16 -45 -66 M
15 24 57 8 24 36 16 -64 -30 -65 M
15 2 -8 -8 -27 -78 -29 -100 16 -47 7 1
31 3 -50 -31 -27 -79 -94 -85 -23 -18 -8 64
20 -22 9 -23 -43 -59 -26 -55 -25 22 90 156
9 -20 15 -46 -70 -2 -41 -36 35 53 67 163 163
-3 -23 -48 -60 -144 -80 -126 -46 44 10 -20 44 178
135 -68 -57 -113 -14 -91 -45 14 16 12 6 46 129
0
-100
-100
-100
0
0
+100

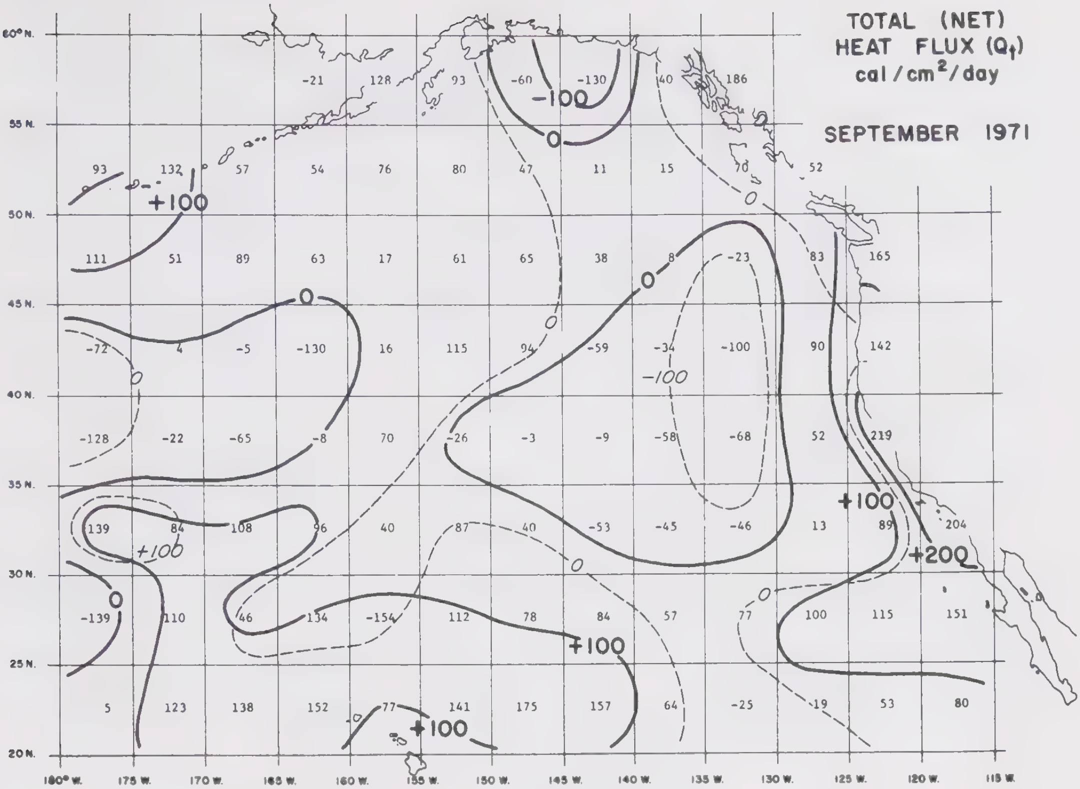

TOTAL (NET) HEAT FLUX (Q_t)
cal / cm²/ day
APRIL 1971
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W
170 W.
165 W
160 W
155 W
150 W
145 W
140 W
135 W
130 W.
125 W
120 W.
115 W.
217 122 134 65 -7 70 87
93 89 85 112 105 146 127 103 154 135 M
116 134 111 67 90 133 117 93 124 152 162 33
106 135 56 140 78 90 19 72 101 185 159 103
125 172 137 134 125 133 8 43 75 105 143 235
157 153 102 115 129 115 78 79 83 65 114 192 215
143 91 149 123 35 64 -4 17 79 58 69 150 220
188 34 -32 1 -116 -69 82 44 -116 -132 -57 55 103
+100
+100
+100
+100
+200
0
-100
-100


TOTAL (NET) HEAT FLUX (Q_t)
cal / cm² / day
MAY 1971
161 131 150 142 123 112 244
190 142 157 241 177 159 228 190 229 257 352
170 196 203 228 193 238 163 210 222 178 172 218
134 116 148 113 122 197 205 198 235 179 160 235
94 62 138 139 136 198 130 169 187 106 202 257
132 92 162 168 217 267 263 150 120 146 125 229 227
45 120 181 238 258 114 120 128 145 139 130 207 192
225 242 265 132 162 141 170 30 74 65 10 75 49
+100
+200
+200
+100
-100
+100
0
60° N
55 N
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q_t)
cal / cm² / day
JUNE 1971
180 298 289 137 141 141 247
167 165 215 227 211 195 178 203 181 200 219
157 195 206 202 220 249 221 165 141 219 198 240
187 210 222 193 238 174 143 146 157 196 228 342
155 192 276 267 110 146 173 162 177 240 247 308
283 253 266 146 172 203 143 171 188 196 208 230 201
207 222 287 208 76 168 152 130 127 138 152 190 174
200 247 204 211 71 231 212 110 39 44 155 146 136
+200
+200
+100
+300
+200
-100
0
+200
+100
+100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


TOTAL (NET) HEAT FLUX (Q$_t$) cal / cm² / day
JULY 1971
60° N
55 N.
50 N.
45 N
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
154 74 300 191 134 93 389
151 152 166 161 200 174 237 167 123 217 283
213 149 200 194 206 232 215 164 184 177 230 105
167 163 199 228 199 174 190 203 168 160 225 293
237 205 258 184 217 259 249 216 199 184 122 344
315 312 260 158 218 220 212 217 186 192 138 191 150
131 193 208 113 145 127 101 91 118 63 105 113 210
147 221 194 153 209 167 70 -6 -48 -83 -11 51 158
+200
+200
+200
+300
+300
+100
+100
0
0
0
0
0
0

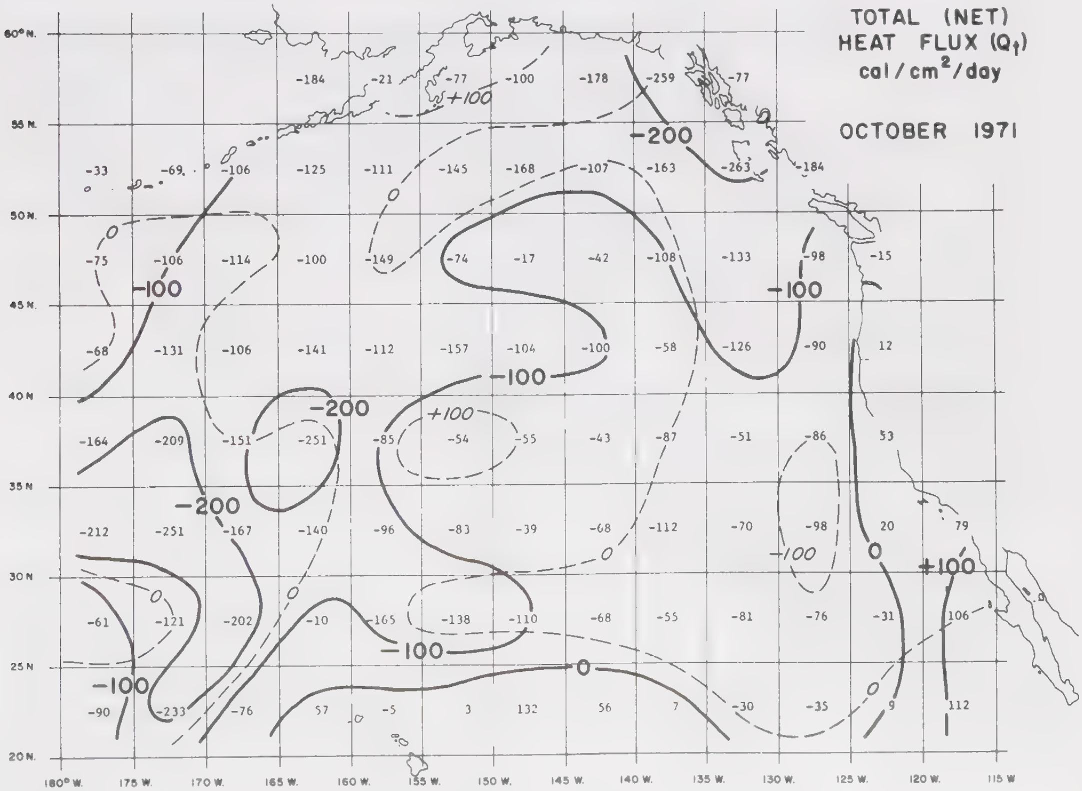

TOTAL (NET) HEAT FLUX (Q$_t$) cal / cm² / day
AUGUST 1971
60° N.
55 N.
50 N.
45 N
40 N.
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
68 156 222 173 46 31 170
152 124 179 197 144 149 120 93 61 102 219
125 160 193 230 233 69 123 73 135 134 194 230
259 261 256 279 170 93 51 69 80 122 219 378
266 279 315 231 111 60 93 93 130 148 320 363
98 174 118 126 125 76 79 187 205 237 290 276 270
29 30 51 51 135 182 134 191 246 237 207 274 261
162 67 26 -6 116 98 72 113 145 71 113 141 240
+100
+100
+100
+100
+100
+200
+200
+200
+300
+300
-100
0
0
0
0



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

SEPTEMBER 1971

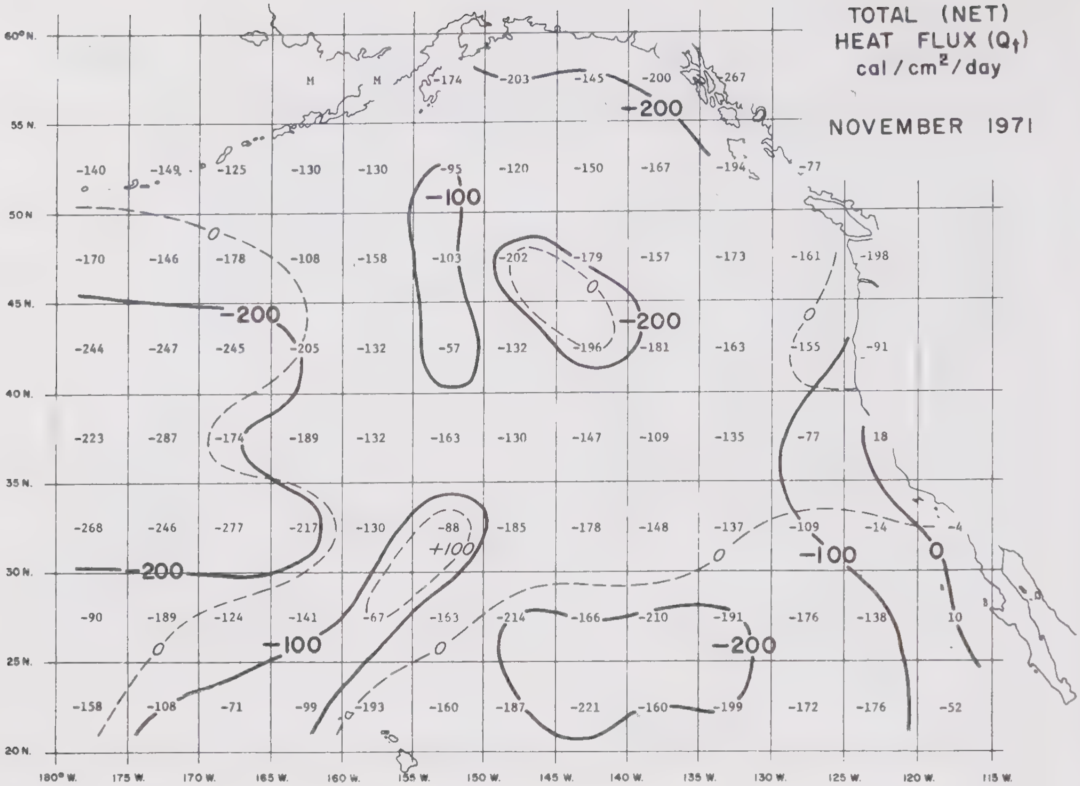
-21
128
93
-60
-130
40
186
-100
0
93
132
57
54
76
80
47
11
15
70
52
+100
0
111
51
89
63
17
61
65
38
8
-23
83
165
0
0
0
-72
4
-5
-130
16
115
94
-59
-34
-100
90
142
0
-100
-128
-22
-65
-8
70
-26
-3
-9
-58
-68
52
219
+100
139
84
108
96
40
87
40
-53
-45
-46
13
89
204
+100
0
+200
0
0
-139
110
46
134
-154
112
78
84
57
77
100
115
151
+100
5
123
138
152
77
141
175
157
64
-25
-19
53
80
+100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

OCTOBER 1971

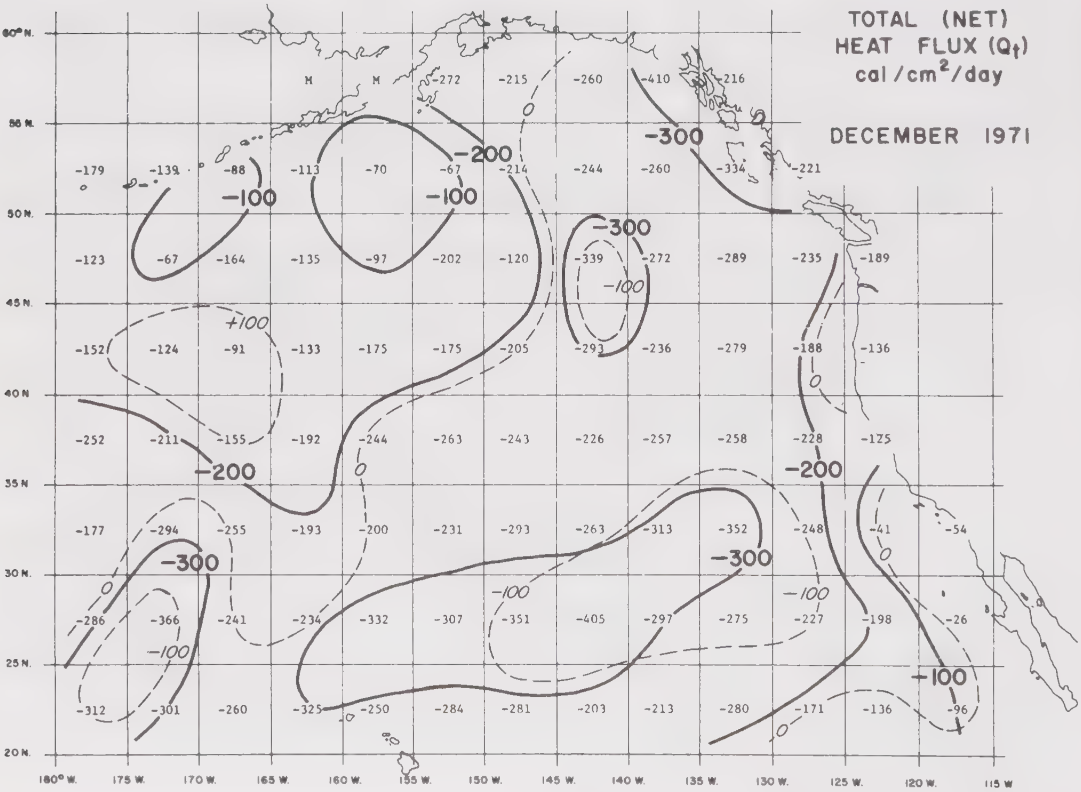
-184
-21
-77
+100
-100
-178
-259
-77
-200
-33
-69
-106
-125
-111
-145
-168
-107
-163
-263
-184
0
0
-75
-106
-114
-100
-149
-74
-17
-42
-108
-133
-98
-15
-100
-100
-68
-131
-106
-141
-112
-157
-104
-100
-58
-126
-90
12
-100
-200
+100
-164
-209
-151
-251
-85
-54
-55
-43
-87
-51
-86
53
-200
-212
-251
-167
-140
-96
-83
-39
-68
-112
-70
-98
20
79
0
-100
0
+100
0
0
-61
-121
-202
-10
-165
-138
-110
-68
-55
-81
-76
-31
106
-100
0
-100
0
-90
-233
-76
57
-5
3
132
56
7
-30
-35
9
112
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

NOVEMBER 1971

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M
M
-174
-203
-145
-200
-267
-200
-140
-149
-125
-130
-130
-95
-120
-150
-167
-194
-77
-100
-170
-146
-178
-108
-158
-103
-202
-179
-157
-173
-161
-198
0
0
-200
-244
-247
-245
-205
-132
-57
-132
-196
-181
-163
-155
-91
-200
0
-223
-287
-174
-189
-132
-163
-130
-147
-109
-135
-77
18
-268
-246
-277
-217
-130
-88
-185
-178
-148
-137
-109
-14
-4
+100
-200
0
-100
0
-90
-189
-124
-141
-67
-163
-214
-166
-210
-191
-176
-138
10
0
-100
0
-200
-158
-108
-71
-99
-193
-160
-187
-221
-160
-199
-172
-176
-52

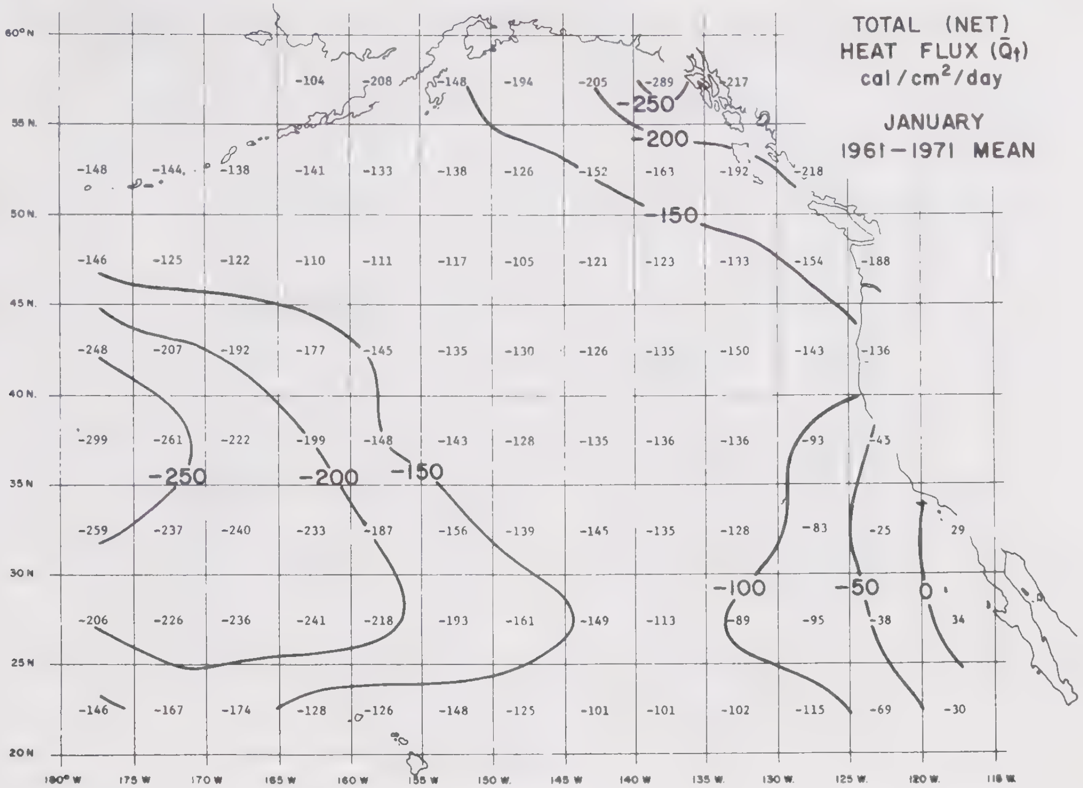


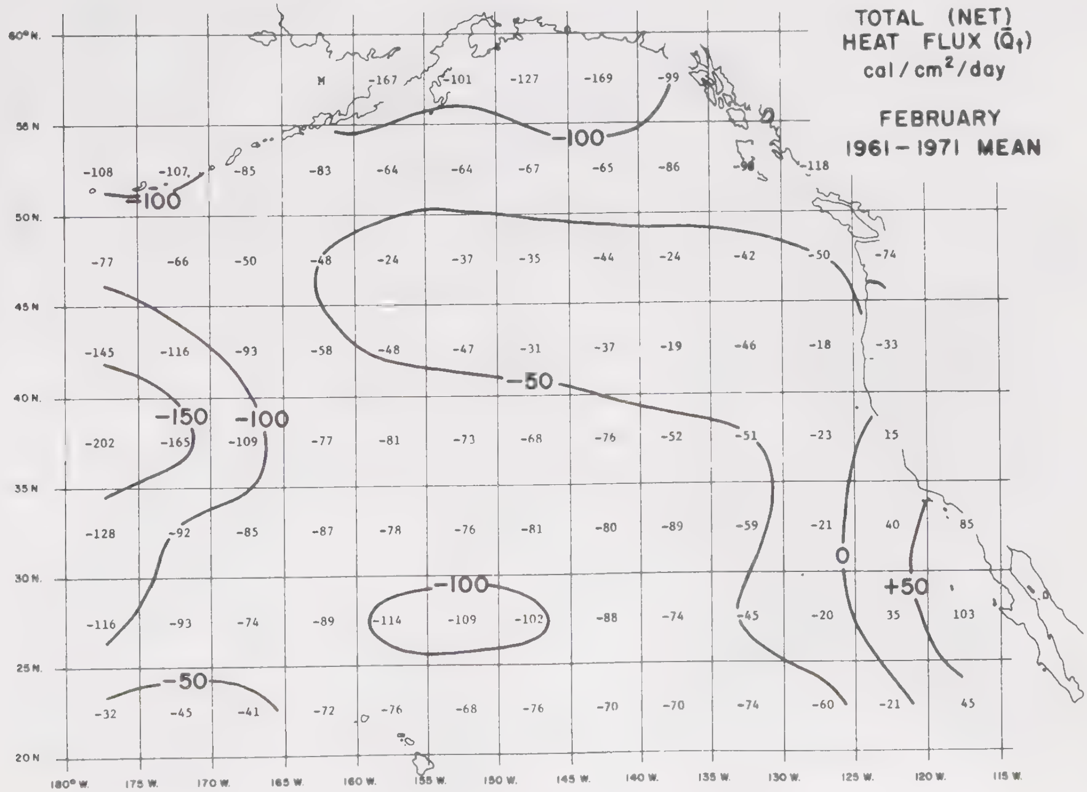
TOTAL (NET) HEAT FLUX (Q_t) cal/cm^2/day

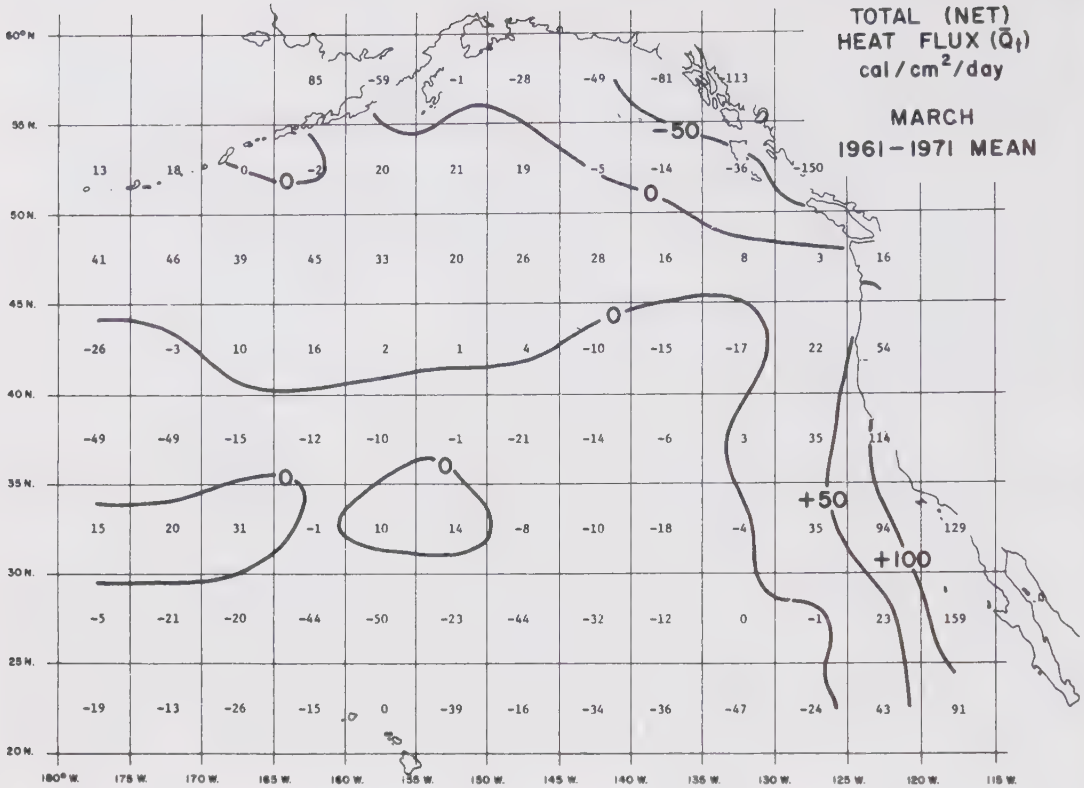
DECEMBER 1971

60° N.
55 N.
50 N.
45 N.
40 N
35 N
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
M
M
-272
-215
0
-260
-410
-216
-300
-200
-179
-139
-88
-113
-70
-67
-214
-244
-260
-334
-221
-100
-100
-300
-123
-67
-164
-135
-97
-202
-120
-339
-272
-289
-235
-189
-100
+100
-152
-124
-91
-133
-175
-175
-205
-293
-236
-279
-188
-136
0
-252
-211
-155
-192
-244
-263
-243
-226
-257
-258
-228
-175
-200
0
-200
-177
-294
-255
-193
-200
-231
-293
-263
-313
-352
-248
-41
-54
-300
-300
0
0
-100
-100
-286
-366
-241
-234
-332
-307
-351
-405
-297
-275
-227
-198
-26
-100
-100
-312
-301
-260
-325
-250
-284
-281
-203
-213
-280
-171
-136
-96
0

PART 2. TOTAL (NET) HEAT FLUX 1961-71 MEAN MONTHLY VALUES (NORMALS).


TOTAL (NET)
HEAT FLUX ($\bar{Q}_t$)
cal/cm²/day
JANUARY
1961–1971 MEAN
60° N
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N
20 N
180° W
175 W
170 W
165 W
160 W
155 W
150 W.
145 W
140 W
135 W.
130 W.
125 W.
120 W.
115 W.
-104 -208 -148 -194 -205 -289 -217
-250
-200
-148 -144 -138 -141 -133 -138 -126 -152 -163 -192 -218
-150
-146 -125 -122 -110 -111 -117 -105 -121 -123 -133 -154 -188
-248 -207 -192 -177 -145 -135 -130 -126 -135 -150 -143 -136
-299 -261 -222 -199 -148 -143 -128 -135 -136 -136 -93 -43
-250
-200
-150
-259 -237 -240 -233 -187 -156 -139 -145 -135 -128 -83 -25 29
-100
-50
0
-206 -226 -236 -241 -218 -193 -161 -149 -113 -89 -95 -38 34
-146 -167 -174 -128 -126 -148 -125 -101 -101 -102 -115 -69 -30

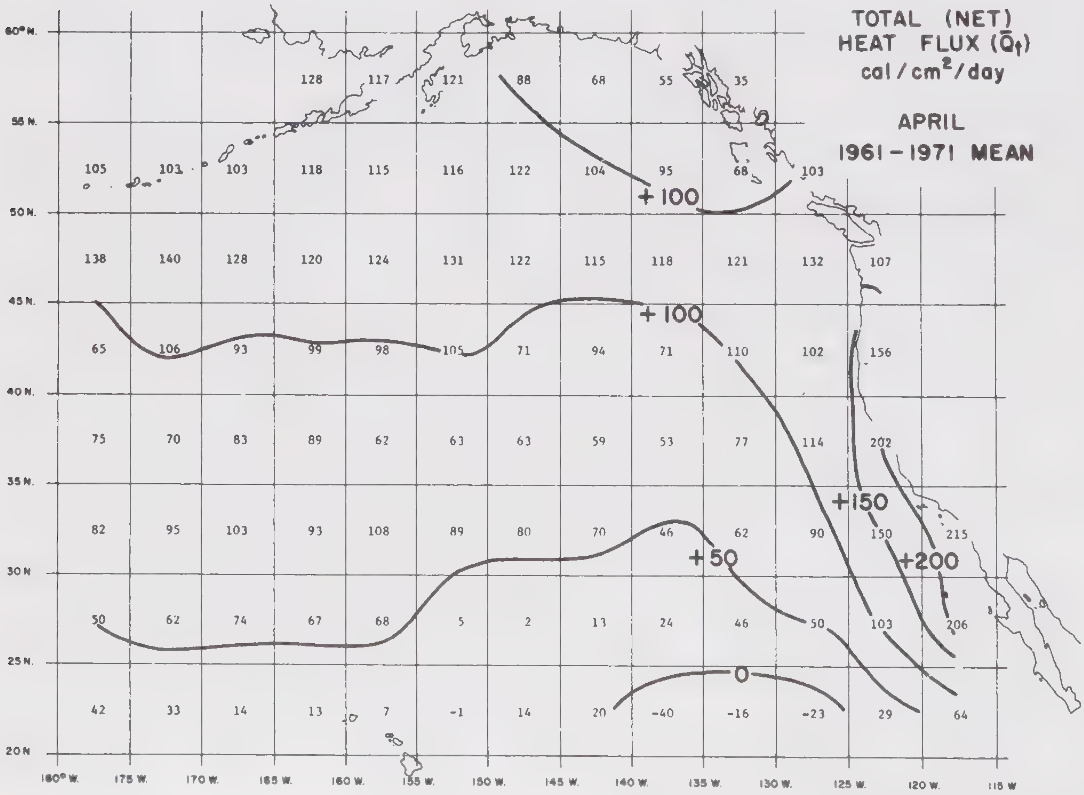

TOTAL (NET)
HEAT FLUX ($\bar{Q}_t$)
cal/cm²/day
FEBRUARY
1961–1971 MEAN
60° N.
55 N
50 N.
45 N
40 N.
35 N
30 N.
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
M -167 -101 -127 -169 -99
-100
-108 -107 -85 -83 -64 -64 -67 -65 -86 -98 -118
-100
-77 -66 -50 -48 -24 -37 -35 -44 -24 -42 -50 -74
-145 -116 -93 -58 -48 -47 -31 -37 -19 -46 -18 -33
-50
-150
-100
-202 -165 -109 -77 -81 -73 -68 -76 -52 -51 -23 15
-128 -92 -85 -87 -78 -76 -81 -80 -89 -59 -21 40 85
0
+50
-100
-116 -93 -74 -89 -114 -109 -102 -88 -74 -45 -20 35 103
-50
-32 -45 -41 -72 -76 -68 -76 -70 -70 -74 -60 -21 45



TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm^2/day

MARCH 1961–1971 MEAN

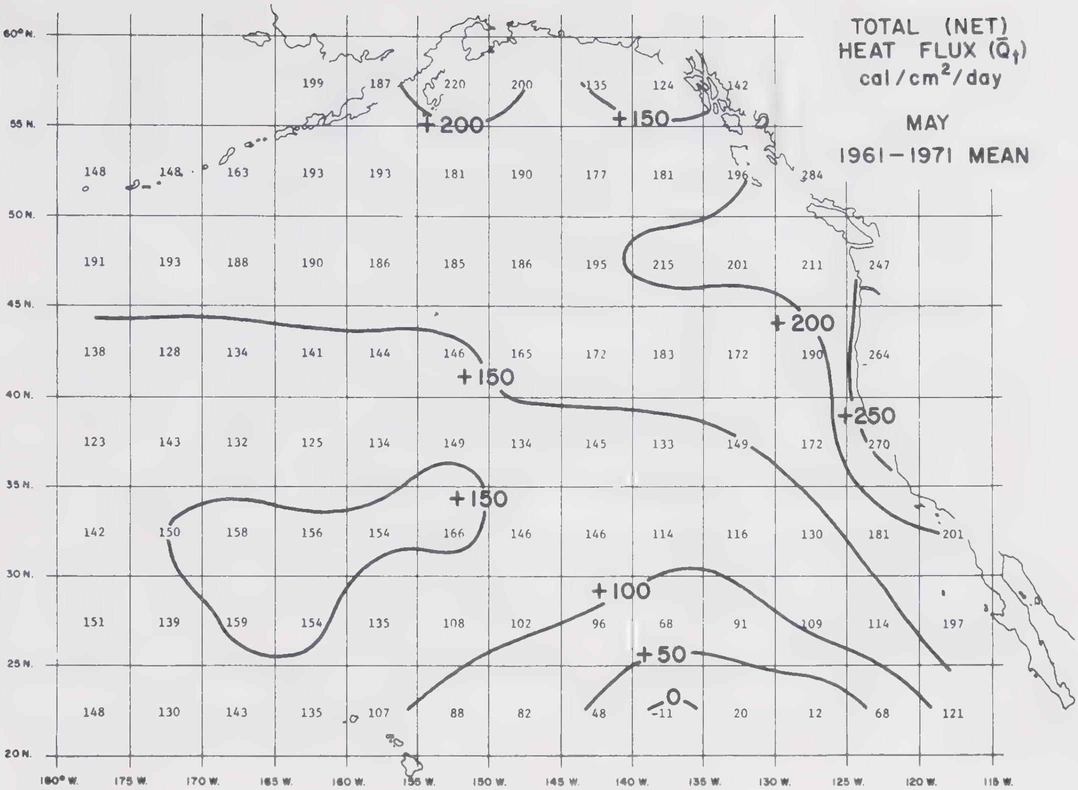
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
85 -59 -1 -28 -49 -81 -113
13 18 0 -2 20 21 19 -5 -14 -36 -150
41 46 39 45 33 20 26 28 16 8 3 16
-26 -3 10 16 2 1 4 -10 -15 -17 22 54
-49 -49 -15 -12 -10 -1 -21 -14 -6 3 35 114
15 20 31 -1 10 14 -8 -10 -18 -4 35 94 129
-5 -21 -20 -44 -50 -23 -44 -32 -12 0 -1 23 159
-19 -13 -26 -15 0 -39 -16 -34 -36 -47 -24 43 91
-50
0
0
0
0
0
0
+50
+100

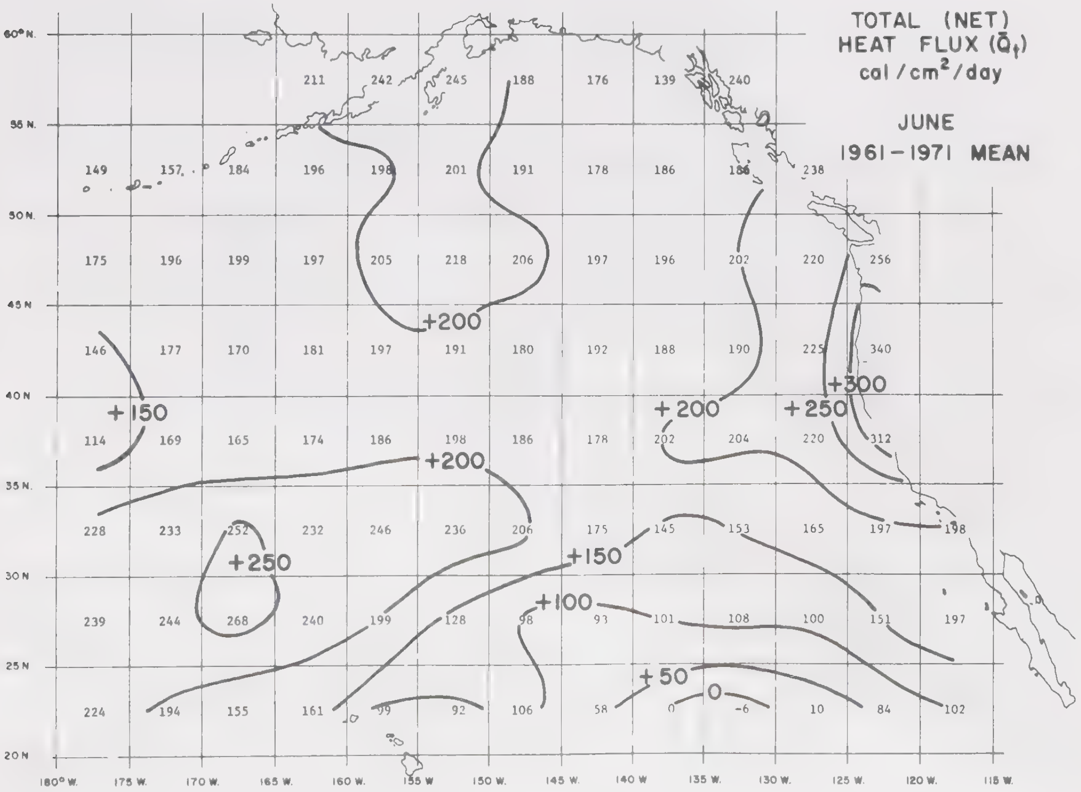


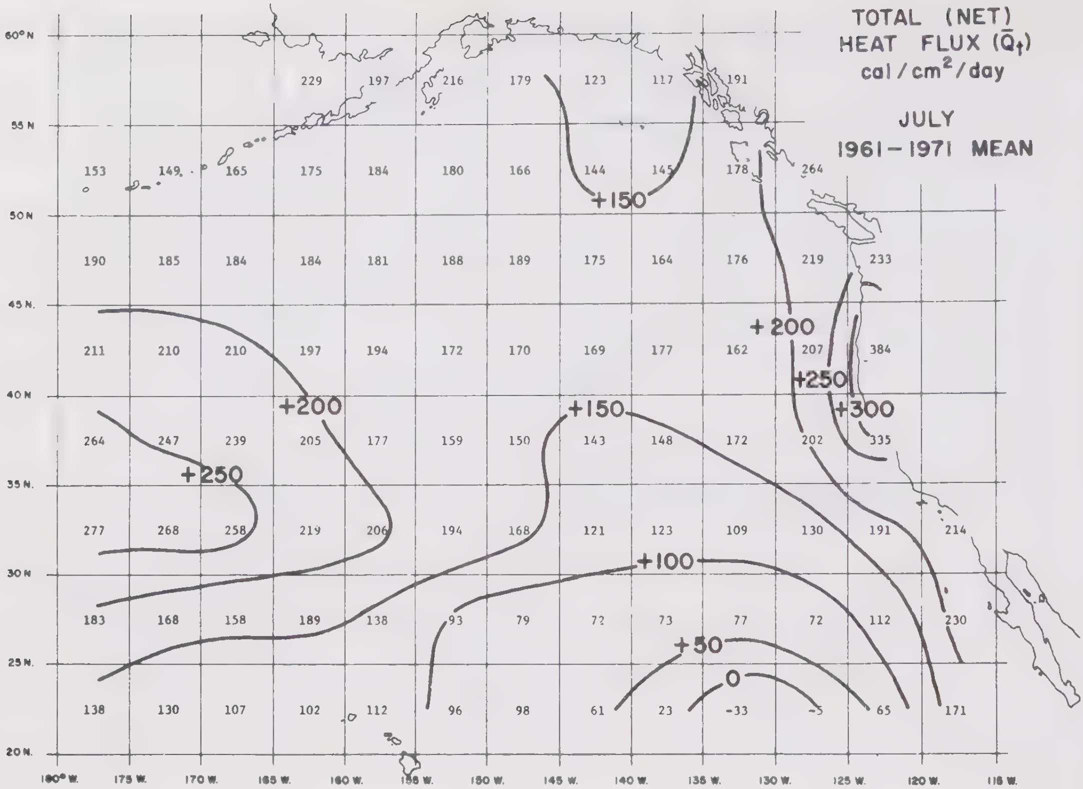
TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm^2/day

APRIL 1961–1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
128 117 121 88 68 55 35
105 103 103 118 115 116 122 104 95 68 103
138 140 128 120 124 131 122 115 118 121 132 107
65 106 93 99 98 105 71 94 71 110 102 156
75 70 83 89 62 63 63 59 53 77 114 202
82 95 103 93 108 89 80 70 46 62 90 150 215
50 62 74 67 68 5 2 13 24 46 50 103 206
42 33 14 13 7 -1 14 20 -40 -16 -23 29 64
+100
+100
+150
+50
+200
0


TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm^2/day
MAY
1961–1971 MEAN
199 187 220 200 135 124 142
148 148 163 193 193 181 190 177 181 196 284
191 193 188 190 186 185 186 195 215 201 211 247
138 128 134 141 144 146 165 172 183 172 190 264
123 143 132 125 134 149 134 145 133 149 172 270
142 150 158 156 154 166 146 146 114 116 130 181 201
151 139 159 154 135 108 102 96 68 91 109 114 197
148 130 143 135 107 88 82 48 -11 20 12 68 121
+200
+150
+200
+150
+250
+150
+100
+50
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

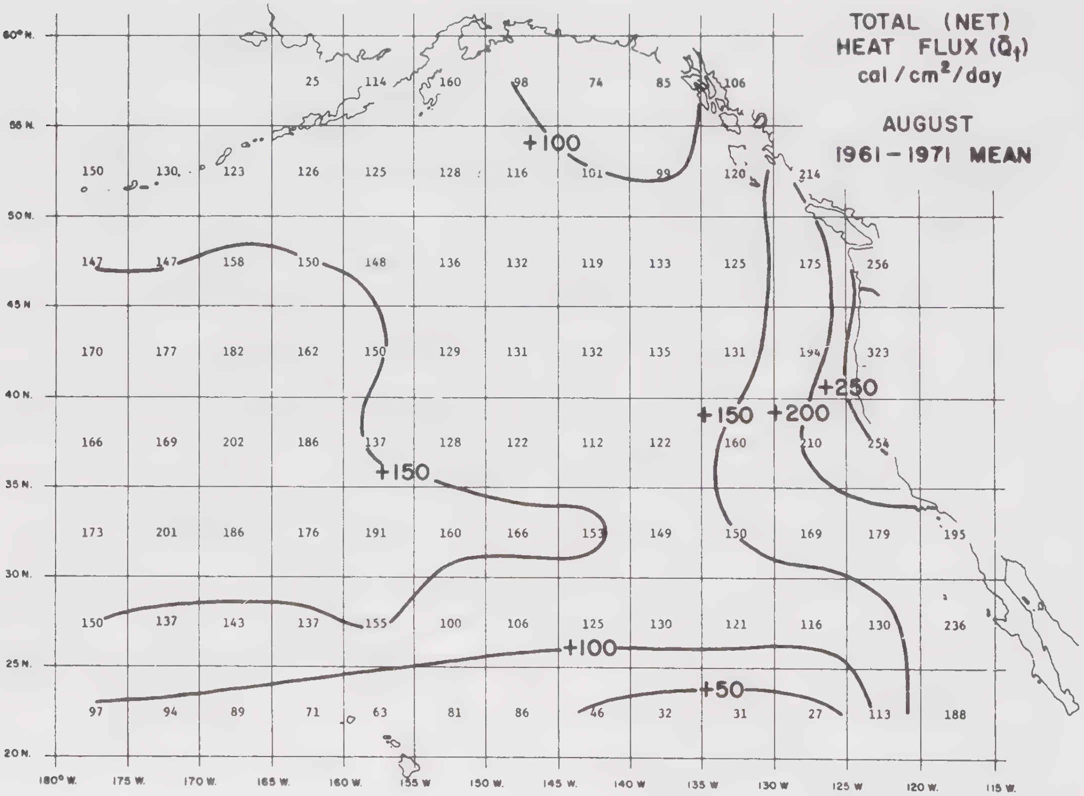

TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm^2/day
JUNE
1961–1971 MEAN
211 242 245 188 176 139 240
149 157 184 196 198 201 191 178 186 186 238
175 196 199 197 205 218 206 197 196 202 220 256
146 177 170 181 197 191 180 192 188 190 225 340
114 169 165 174 186 198 186 178 202 204 220 312
228 233 252 232 246 236 206 175 145 153 165 197 198
239 244 268 240 199 128 98 93 101 108 100 151 197
224 194 155 161 99 92 106 58 0 -6 10 84 102
+200
+150
+300
+250
+200
+200
+250
+150
+100
+50
0
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm²/day

JULY 1961–1971 MEAN

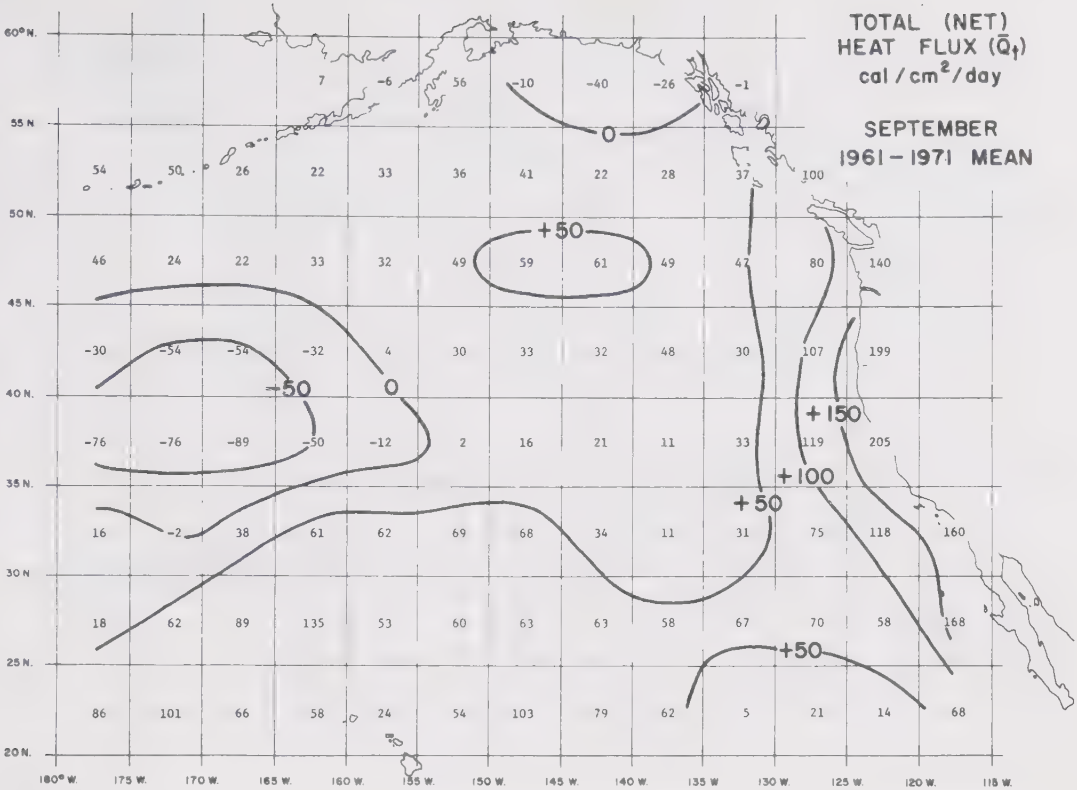
60° N
55 N
50 N
45 N.
40 N
35 N.
30 N
25 N.
20 N.
229 197 216 179 123 117 191
153 149 165 175 184 180 166 144 145 178 264
+150
190 185 184 184 181 188 189 175 164 176 219 233
+200
211 210 210 197 194 172 170 169 177 162 207 384
+250
+200
+150
+300
264 247 239 205 177 159 150 143 148 172 202 335
+250
277 268 258 219 206 194 168 121 123 109 130 191 214
+100
183 168 158 189 138 93 79 72 73 77 72 112 230
+50
0
138 130 107 102 112 96 98 61 23 -33 -5 65 171
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm²/day

AUGUST 1961–1971 MEAN

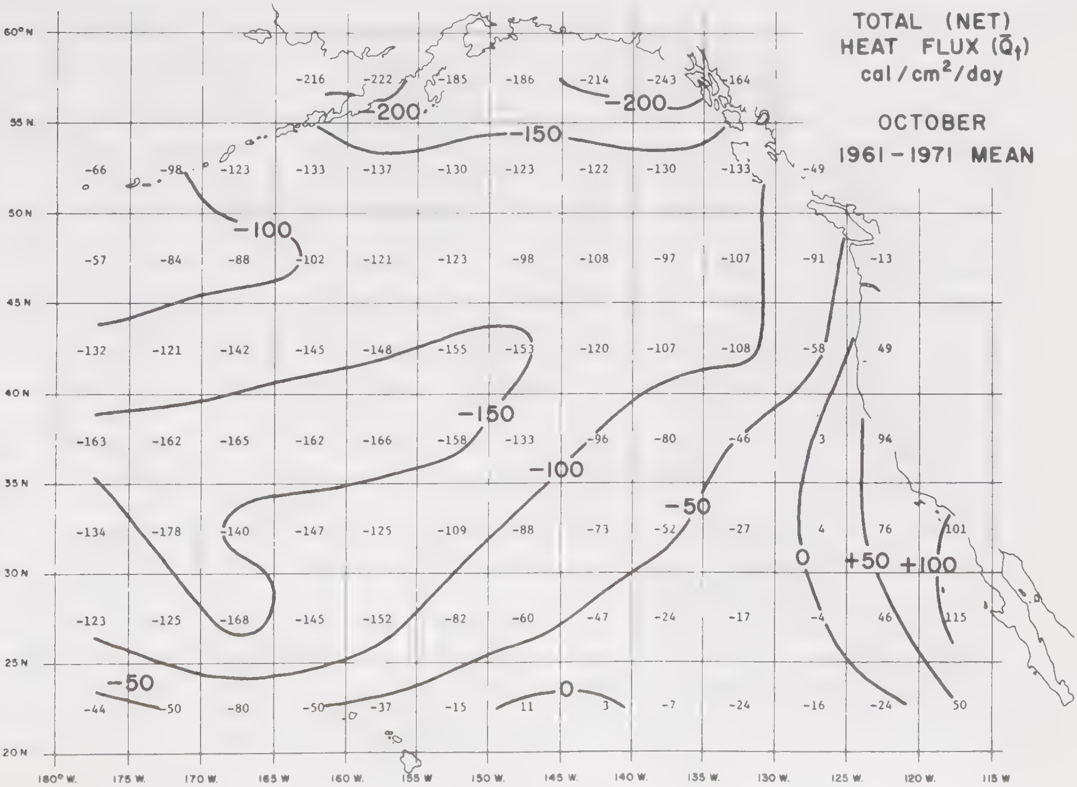
60° N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N.
25 N.
20 N.
25 114 160 98 74 85 106
+100
150 130 123 126 125 128 116 101 99 120 214
147 147 158 150 148 136 132 119 133 125 175 256
170 177 182 162 150 129 131 132 135 131 194 323
+250
+150
+200
166 169 202 186 137 128 122 112 122 160 210 254
+150
173 201 186 176 191 160 166 153 149 150 169 179 195
150 137 143 137 155 100 106 125 130 121 116 130 236
+100
+50
97 94 89 71 63 81 86 46 32 31 27 113 188
180° W.
175 W.
170 W.
165 W.
160 W.
155 W
150 W.
145 W.
140 W
135 W
130 W
125 W
120 W.
115 W.



TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal / cm^2/ day

SEPTEMBER 1961 – 1971 MEAN

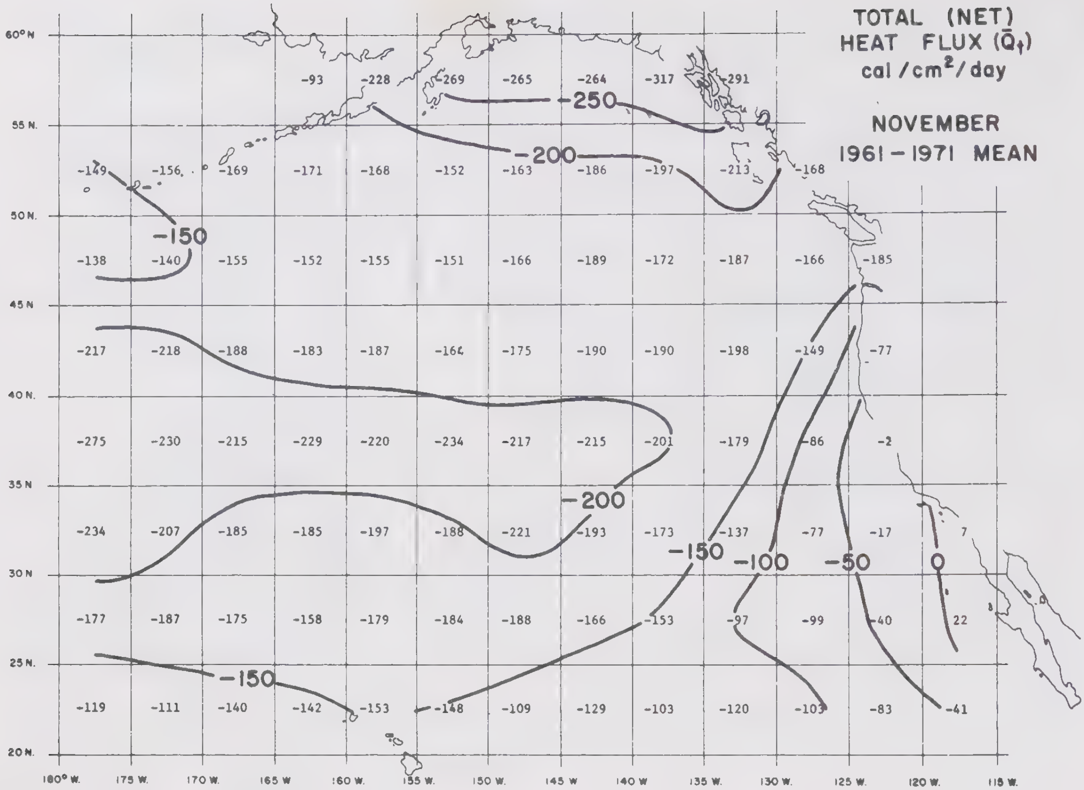
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
7 -6 56 -10 -40 -26 -1
0
54 50 26 22 33 36 41 22 28 37 100
+50
46 24 22 33 32 49 59 61 49 47 80 140
-30 -54 -54 -32 4 30 33 32 48 30 107 199
-50
0
+150
-76 -76 -89 -50 -12 2 16 21 11 33 119 205
+100
+50
16 -2 38 61 62 69 68 34 11 31 75 118 160
18 62 89 135 53 60 63 63 58 67 70 58 168
+50
86 101 66 58 24 54 103 79 62 5 21 14 68
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W
130 W.
125 W.
120 W.
115 W.



TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal / cm^2/ day

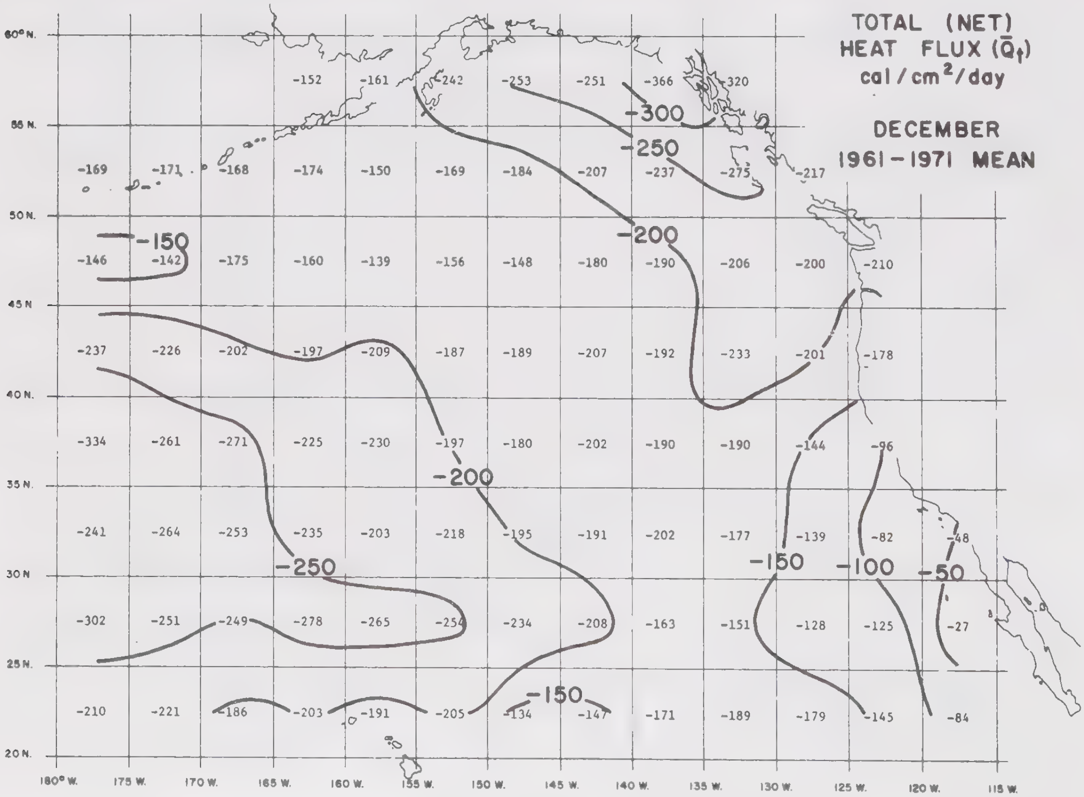
OCTOBER 1961 – 1971 MEAN

60°N
55 N.
50 N
45 N
40 N
35 N
30 N
25 N
20 N
-216 -222 -185 -186 -214 -243 -164
-200
-200
-150
-66 -98 -123 -133 -137 -130 -123 -122 -130 -133 -49
-100
-57 -84 -88 -102 -121 -123 -98 -108 -97 -107 -91 -13
-132 -121 -142 -145 -148 -155 -153 -120 -107 -108 -58 49
-150
-163 -162 -165 -162 -166 -158 -133 -96 -80 -46 3 94
-100
-50
-134 -178 -140 -147 -125 -109 -88 -73 -52 -27 4 76 101
0
+50
+100
-123 -125 -168 -145 -152 -82 -60 -47 -24 -17 -4 46 115
-50
0
-44 -50 -80 -50 -37 -15 11 3 -7 -24 -16 -24 50
180° W.
175 W.
170 W.
165 W
160 W.
155 W
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W


60° N.
55 N.
50 N.
45 N
40 N.
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W
160 W.
155 W.
150 W.
145 W
140 W
135 W.
130 W.
125 W.
120 W.
115 W.
-93 -228 -269 -265 -264 -317 -291
-149 -156 -169 -171 -168 -152 -163 -186 -197 -213 -168
-138 -140 -155 -152 -155 -151 -166 -189 -172 -187 -166 -185
-217 -218 -188 -183 -187 -164 -175 -190 -190 -198 -149 -77
-275 -230 -215 -229 -220 -234 -217 -215 -201 -179 -86 -2
-234 -207 -185 -185 -197 -188 -221 -193 -173 -137 -77 -17 7
-177 -187 -175 -158 -179 -184 -188 -166 -153 -97 -99 -40 22
-119 -111 -140 -142 -153 -148 -109 -129 -103 -120 -103 -83 -41
-250
-200
-150
-200
-150
-100
-50
0
-150

TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm²/day

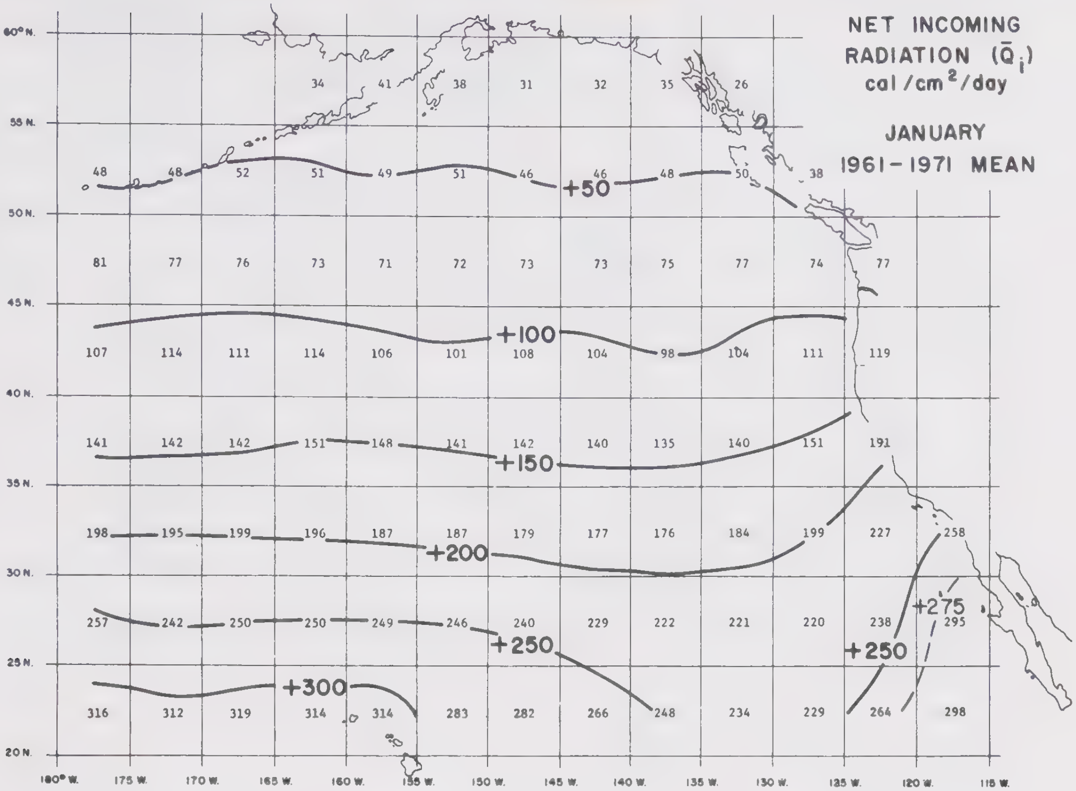
NOVEMBER 1961 – 1971 MEAN


60° N.
55 N.
50 N.
45 N
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-152 -161 -242 -253 -251 -366 -320
-169 -171 -168 -174 -150 -169 -184 -207 -237 -275 -217
-146 -142 -175 -160 -139 -156 -148 -180 -190 -206 -200 -210
-237 -226 -202 -197 -209 -187 -189 -207 -192 -233 -201 -178
-334 -261 -271 -225 -230 -197 -180 -202 -190 -190 -144 -96
-241 -264 -253 -235 -203 -218 -195 -191 -202 -177 -139 -82 -48
-302 -251 -249 -278 -265 -254 -234 -208 -163 -151 -128 -125 -27
-210 -221 -186 -203 -191 -205 -134 -147 -171 -189 -179 -145 -84
-300
-250
-150
-200
-200
-250
-150
-150
-100
-50

TOTAL (NET) HEAT FLUX ($\bar{Q}_t$) cal/cm²/day

DECEMBER 1961 – 1971 MEAN

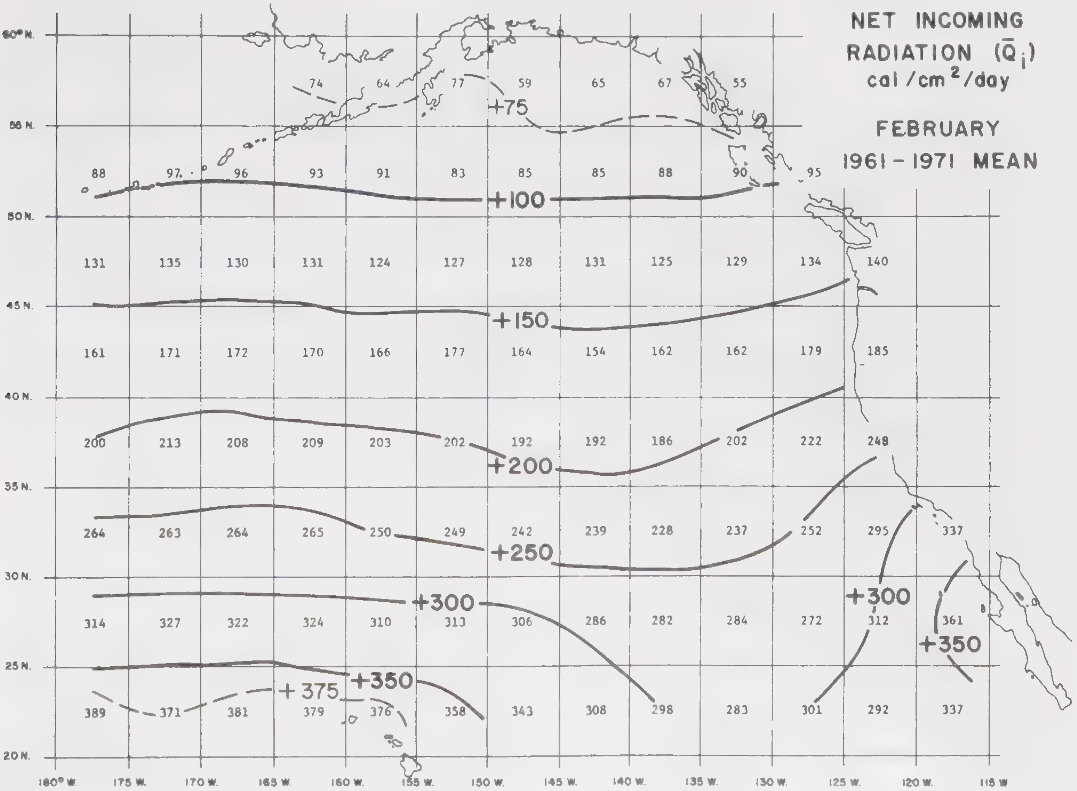
PART 3. NET INCOMING RADIATION 1961-71 MEAN MONTHLY VALUES (NORMALS).



NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

JANUARY 1961-1971 MEAN

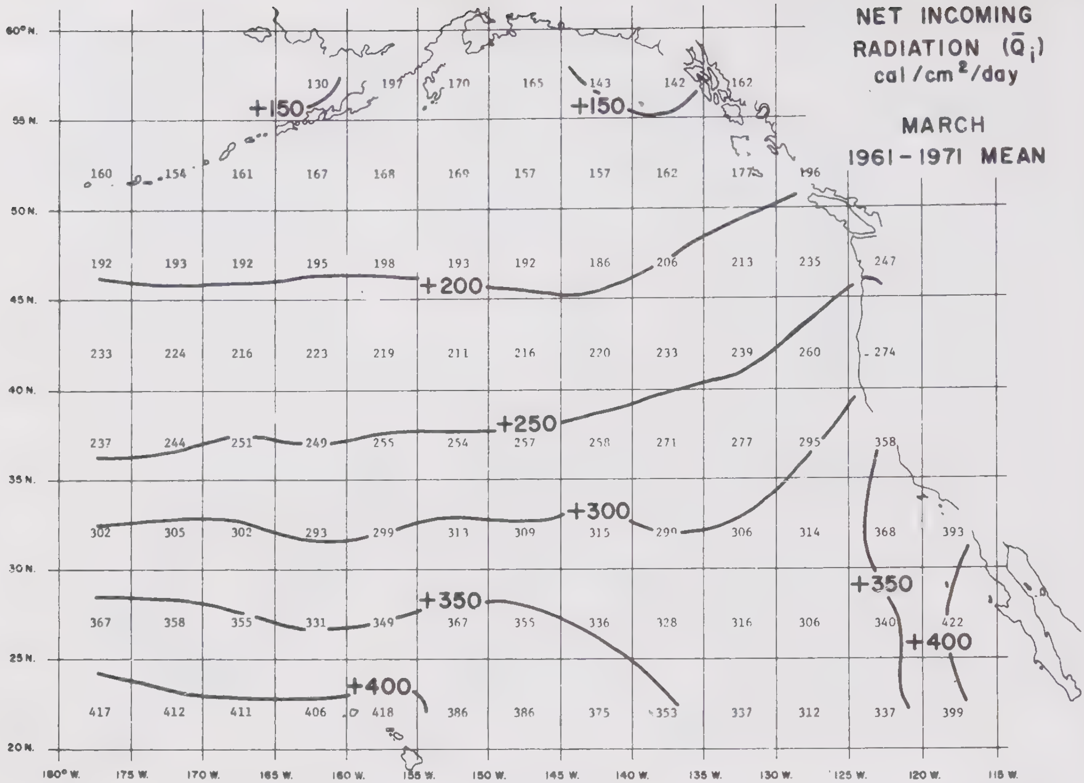
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
34 41 38 31 32 35 26
48 48 52 51 49 51 46 46 48 50 38
+50
81 77 76 73 71 72 73 73 75 77 74 77
+100
107 114 111 114 106 101 108 104 98 104 111 119
141 142 142 151 148 141 142 140 135 140 151 191
+150
198 195 199 196 187 187 179 177 176 184 199 227 258
+200
257 242 250 250 249 246 240 229 222 221 220 238 295
+275
+250
+250
+300
316 312 319 314 314 283 282 266 248 234 229 264 298



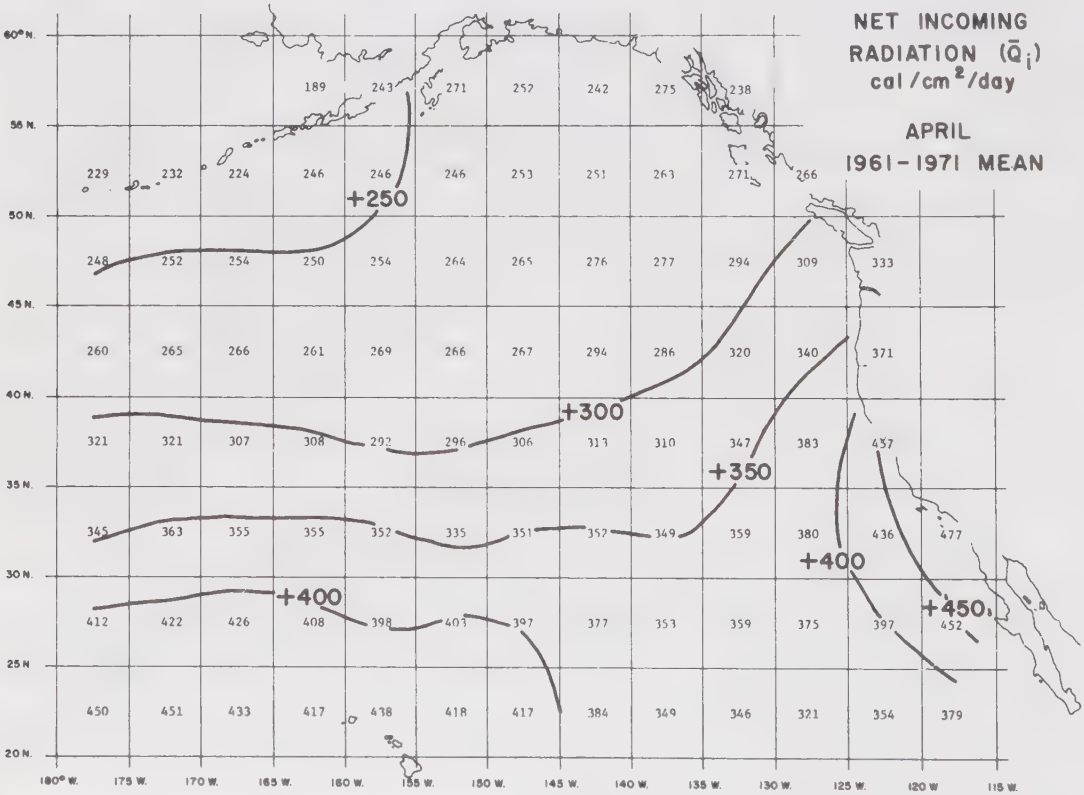
NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

FEBRUARY 1961-1971 MEAN

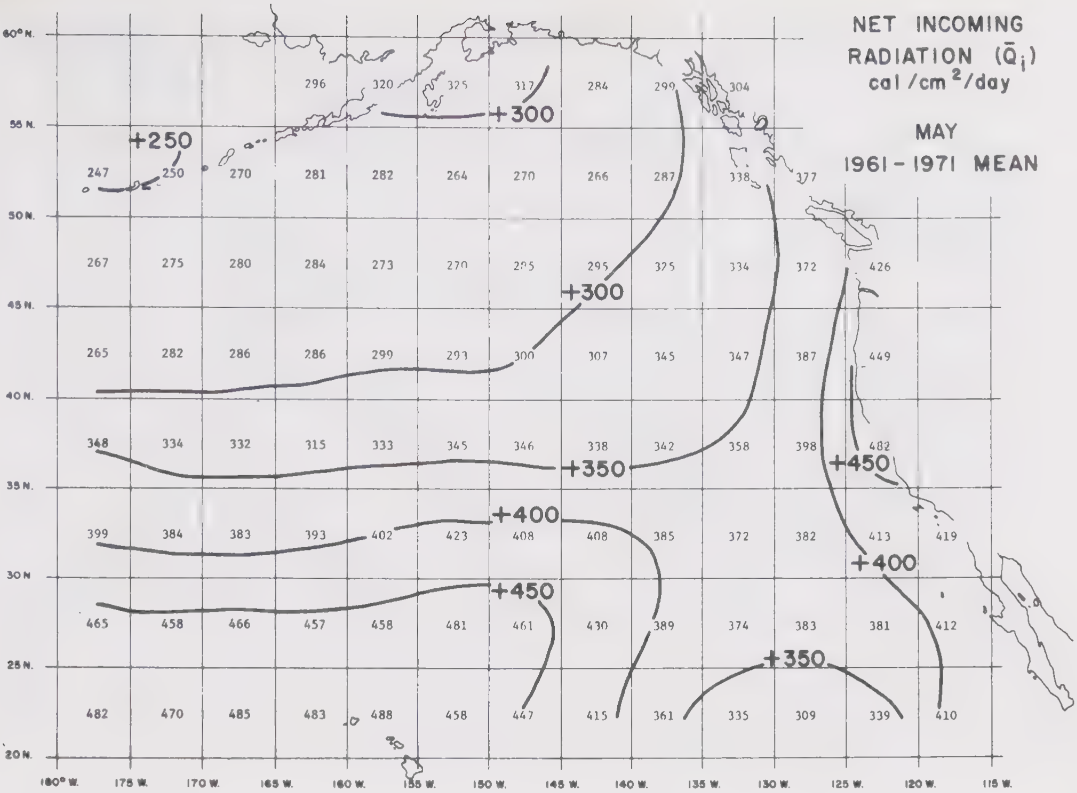
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
74 64 77 59 65 67 55
+75
88 97 96 93 91 83 85 85 88 90 95
+100
131 135 130 131 124 127 128 131 125 129 134 140
+150
161 171 172 170 166 177 164 154 162 162 179 185
200 213 208 209 203 202 192 192 186 202 222 248
+200
264 263 264 265 250 249 242 239 228 237 252 295 337
+250
+300
314 327 322 324 310 313 306 286 282 284 272 312 361
+300
+350
+350
+375
389 371 381 379 376 358 343 308 298 283 301 292 337



NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm²/day
MARCH
1961-1971 MEAN
+150
+150
+200
+250
+300
+350
+350
+400
+400
130 197 170 165 143 142 162
160 154 161 167 168 169 157 157 162 177 196
192 193 192 195 198 193 192 186 206 213 235 247
233 224 216 223 219 211 216 220 233 239 260 274
237 244 251 249 255 254 257 258 271 277 295 358
302 305 302 293 299 313 309 315 290 306 314 368 393
367 358 355 331 349 367 355 336 328 316 306 340 422
417 412 411 406 418 386 386 375 353 337 312 337 399
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

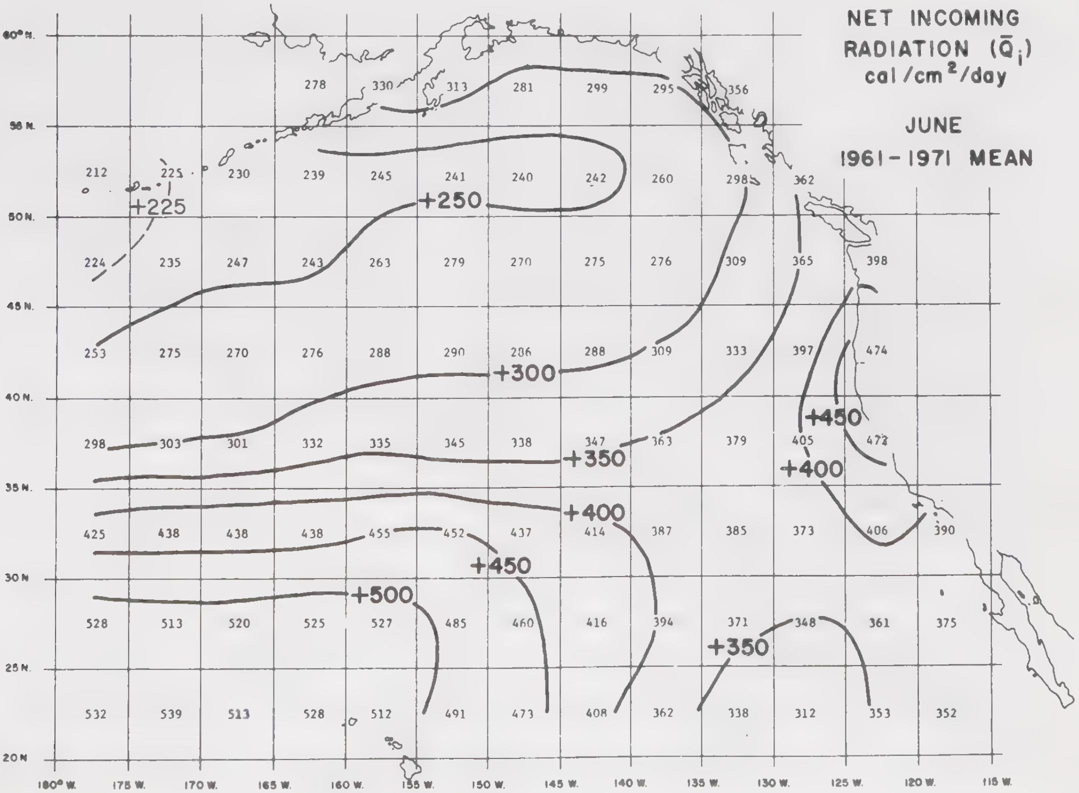


NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm²/day
APRIL
1961-1971 MEAN
+250
+300
+350
+400
+400
+450
189 243 271 252 242 275 238
229 232 224 246 246 246 253 251 263 271 266
248 252 254 250 254 264 265 276 277 294 309 333
260 265 266 261 269 266 267 294 286 320 340 371
321 321 307 308 292 296 306 313 310 347 383 437
345 363 355 355 352 335 351 352 349 359 380 436 477
412 422 426 408 398 403 397 377 353 359 375 397 452
450 451 433 417 438 418 417 384 349 346 321 354 379
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W
115 W.


NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

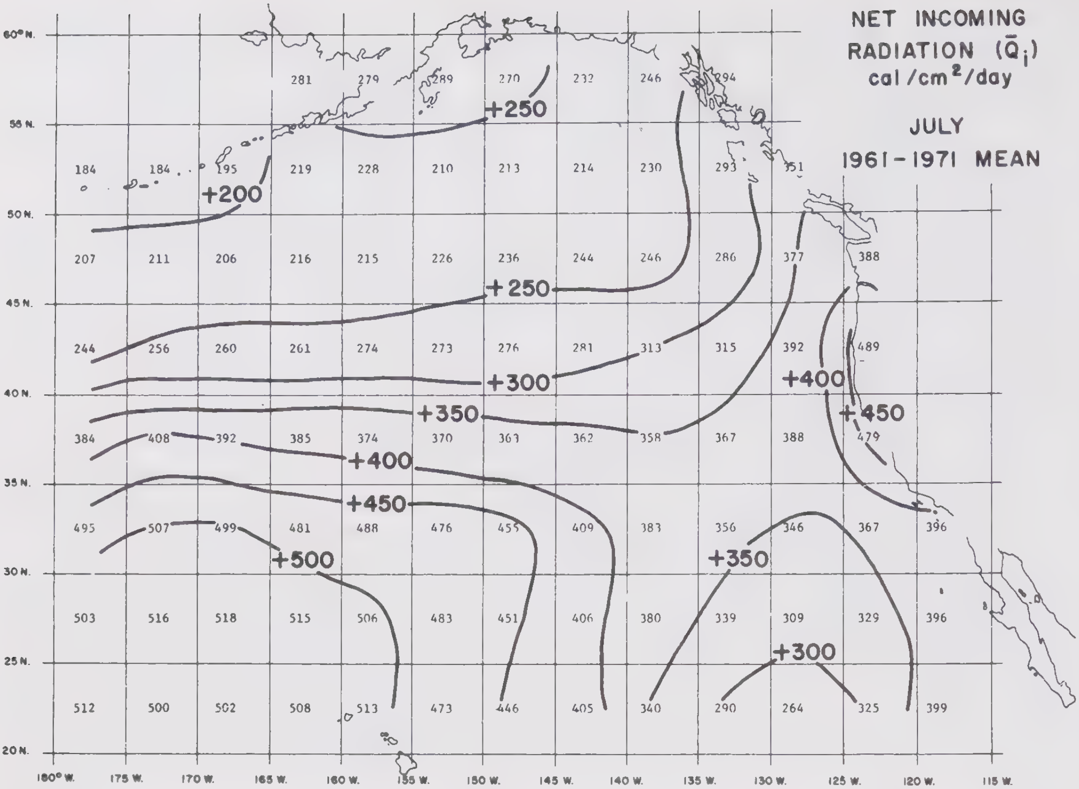
MAY 1961-1971 MEAN

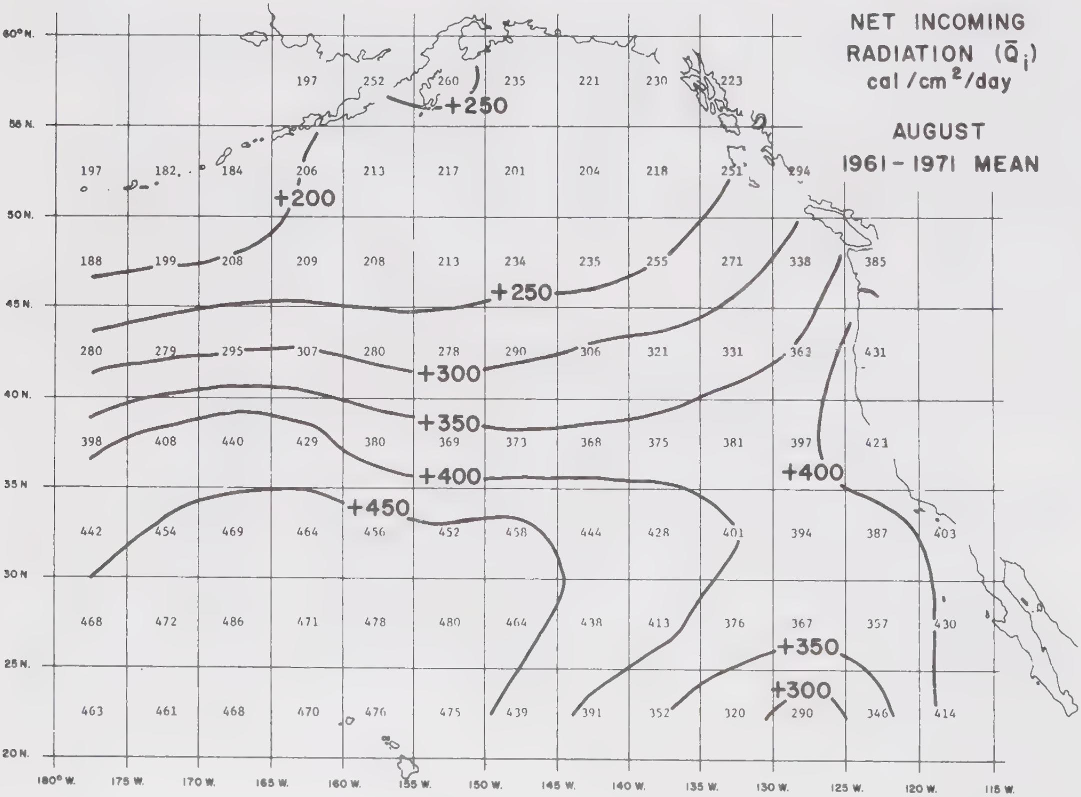
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
296 320 325 317 284 299 304
247 250 270 281 282 264 270 266 287 338 377
267 275 280 284 273 270 295 295 325 334 372 426
265 282 286 286 299 293 300 307 345 347 387 449
348 334 332 315 333 345 346 338 342 358 398 482
399 384 383 393 402 423 408 408 385 372 382 413 419
465 458 466 457 458 481 461 430 389 374 383 381 412
482 470 485 483 488 458 447 415 361 335 309 339 410
+250
+300
+300
+350
+400
+450
+450
+400
+350

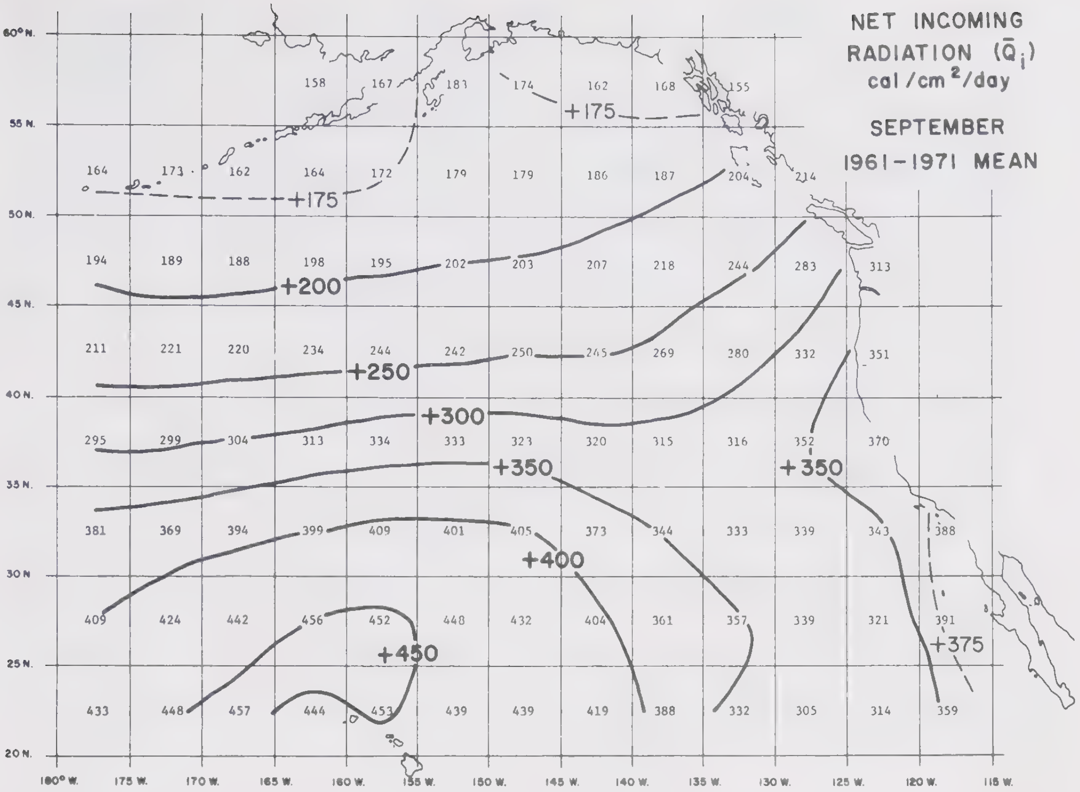

NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

JUNE 1961-1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
278 330 313 281 299 295 356
212 225 230 239 245 241 240 242 260 298 362
224 235 247 243 263 279 270 275 276 309 365 398
253 275 270 276 288 290 286 288 309 333 397 474
298 303 301 332 335 345 338 347 363 379 405 472
425 438 438 438 455 452 437 414 387 385 373 406 390
528 513 520 525 527 485 460 416 394 371 348 361 375
532 539 513 528 512 491 473 408 362 338 312 353 352
+225
+250
+300
+350
+400
+450
+500
+450
+400
+350


NET INCOMING RADIATION ($\bar{Q}_i$) cal /cm^2/day
JULY
1961-1971 MEAN
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
281 279 289 270 232 246 294
184 184 195 219 228 210 213 214 230 293 351
207 211 206 216 215 226 236 244 246 286 377 388
244 256 260 261 274 273 276 281 313 315 392 489
384 408 392 385 374 370 363 362 358 367 388 479
495 507 499 481 488 476 455 409 383 356 346 367 396
503 516 518 515 506 483 451 406 380 339 309 329 396
512 500 502 508 513 473 446 405 340 290 264 325 399
+250
+200
+250
+300
+350
+400
+450
+500
+400
+450
+350
+300


NET INCOMING RADIATION ($\bar{Q}_i$) cal /cm^2/day
AUGUST
1961-1971 MEAN
60° N.
55 N.
50 N.
45 N.
40 N.
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
197 252 260 235 221 230 223
197 182 184 206 213 217 201 204 218 251 294
188 199 208 209 208 213 234 235 255 271 338 385
280 279 295 307 280 278 290 306 321 331 363 431
398 408 440 429 380 369 373 368 375 381 397 423
442 454 469 464 456 452 458 444 428 401 394 387 403
468 472 486 471 478 480 464 438 413 376 367 357 430
463 461 468 470 476 475 439 391 352 320 290 346 414
+250
+200
+250
+300
+350
+400
+450
+400
+350
+300

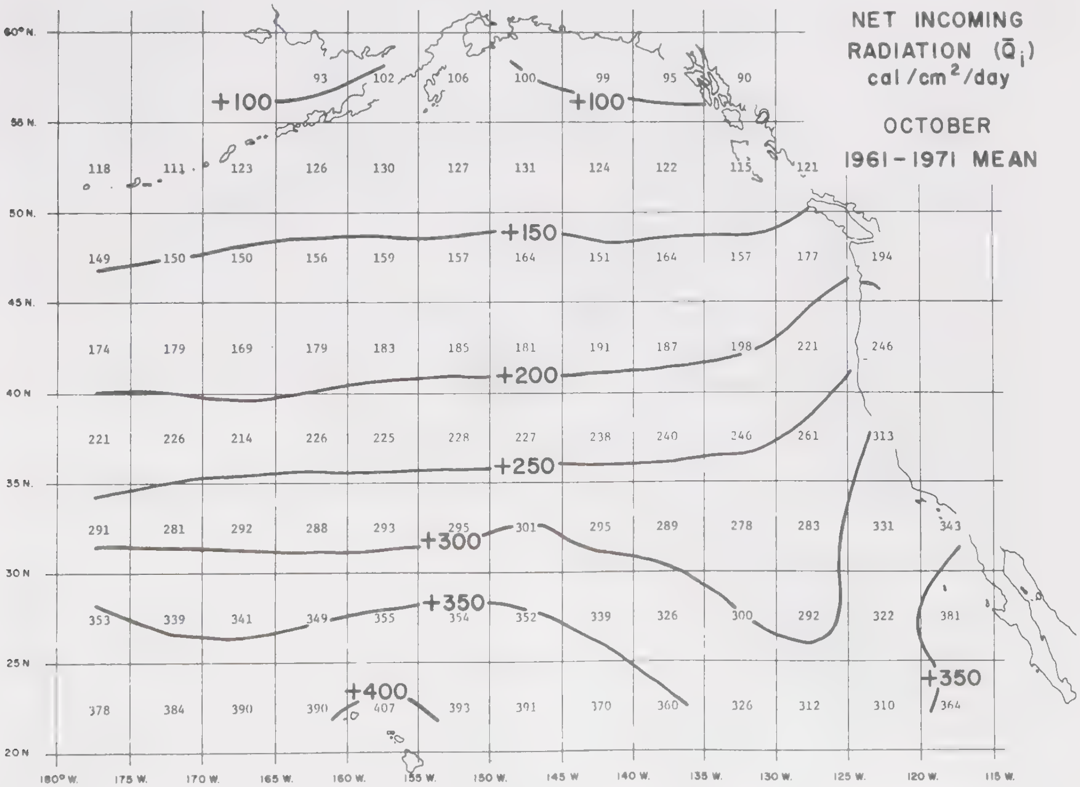


NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

SEPTEMBER

1961-1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
158 167 183 174 162 168 155
+175
164 173 162 164 172 179 179 186 187 204 214
+175
194 189 188 198 195 202 203 207 218 244 283 313
+200
211 221 220 234 244 242 250 245 269 280 332 351
+250
+300
295 299 304 313 334 333 323 320 315 316 352 370
+350
+350
381 369 394 399 409 401 405 373 344 333 339 343 388
+400
409 424 442 456 452 448 432 404 361 357 339 321 391
+450
+375
433 448 457 444 453 439 439 419 388 332 305 314 359

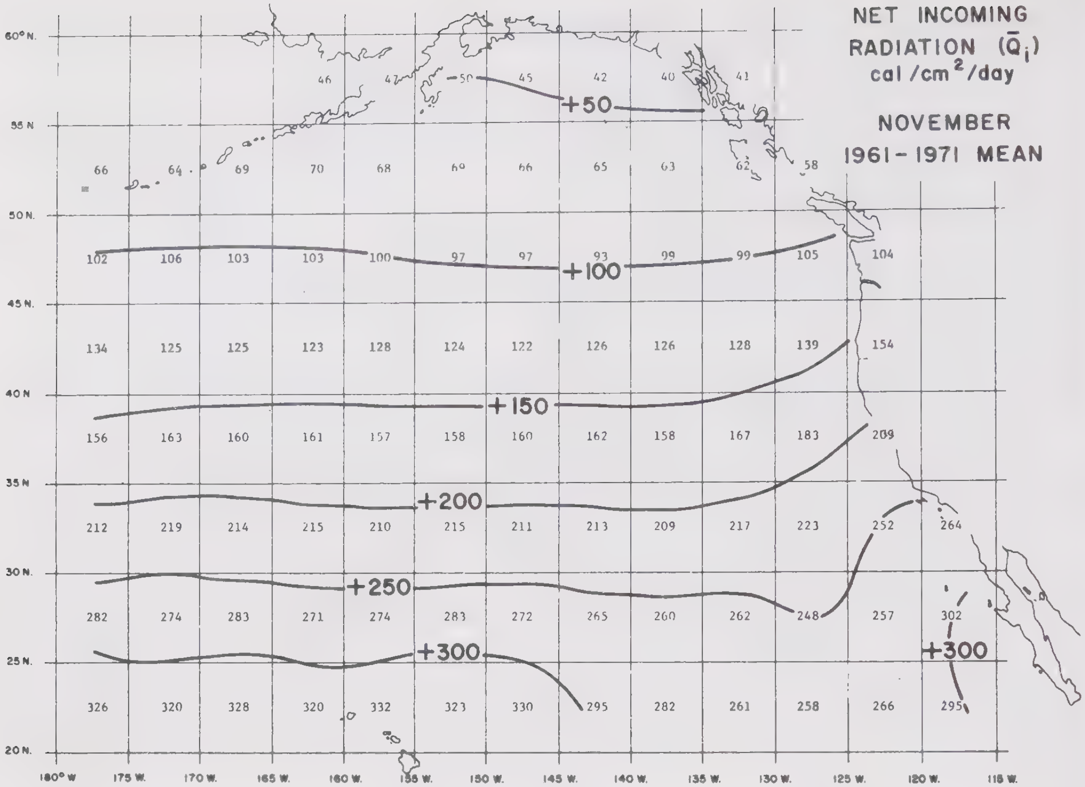


NET INCOMING RADIATION ($\bar{Q}_i$) cal/cm^2/day

OCTOBER

1961-1971 MEAN

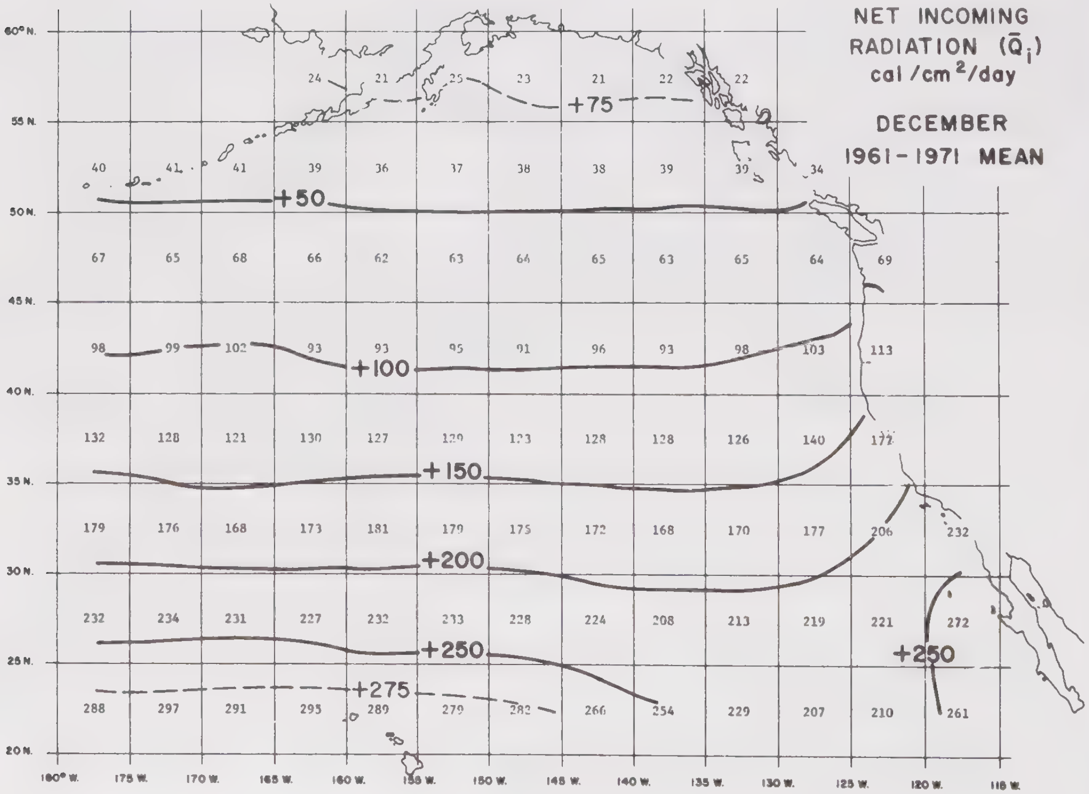
60° N.
55 N.
50 N.
45 N.
40 N
35 N.
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
93 102 106 100 99 95 90
+100
+100
118 111 123 126 130 127 131 124 122 115 121
+150
149 150 150 156 159 157 164 151 164 157 177 194
174 179 169 179 183 185 181 191 187 198 221 246
+200
221 226 214 226 225 228 227 238 240 246 261 313
+250
291 281 292 288 293 295 301 295 289 278 283 331 343
+300
353 339 341 349 355 354 352 339 326 300 292 322 381
+350
+400
+350
378 384 390 390 407 393 391 370 360 326 312 310 364



NET INCOMING RADIATION ($\bar{Q}_i$) cal /cm^2/day

NOVEMBER 1961-1971 MEAN

60° N.
55 N
50 N.
45 N.
40 N
35 N
30 N.
25 N.
20 N.
180° W
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
46 47 50 45 42 40 41
+50
66 64 69 70 68 69 66 65 63 62 58
102 106 103 103 100 97 97 93 99 99 105 104
+100
134 125 125 123 128 124 122 126 126 128 139 154
+150
156 163 160 161 157 158 160 162 158 167 183 209
+200
212 219 214 215 210 215 211 213 209 217 223 252 264
+250
282 274 283 271 274 283 272 265 260 262 248 257 302
+300
+300
326 320 328 320 332 323 330 295 282 261 258 266 295

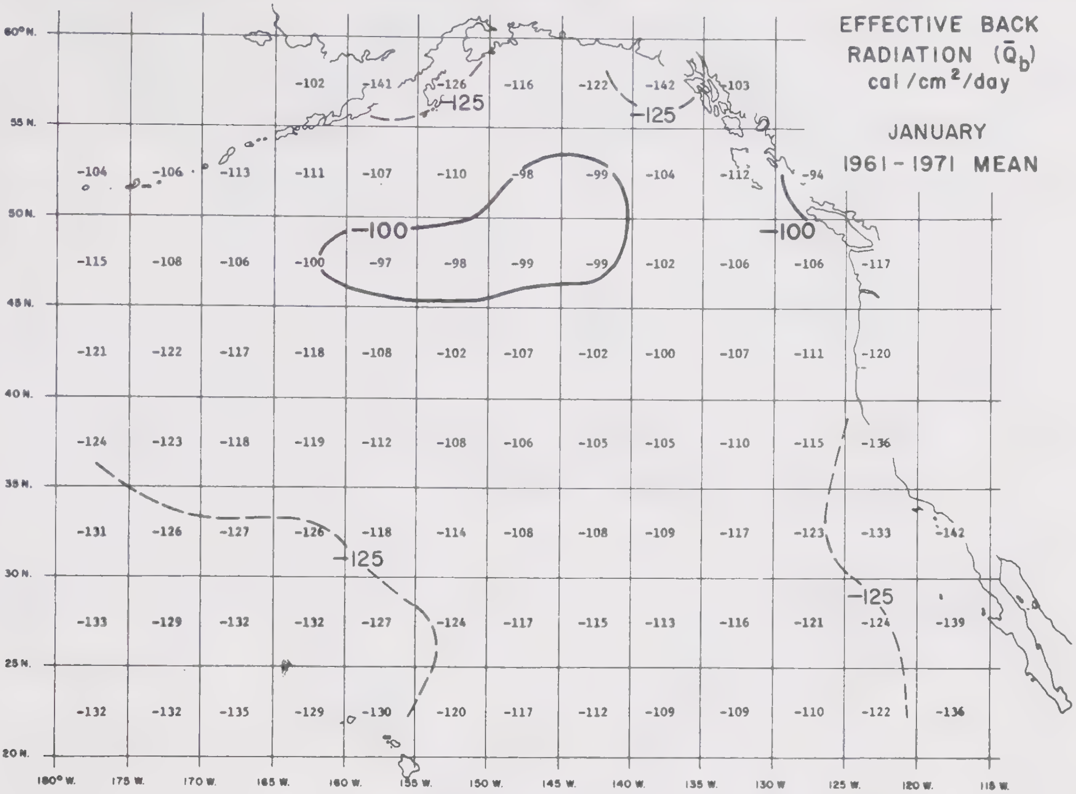


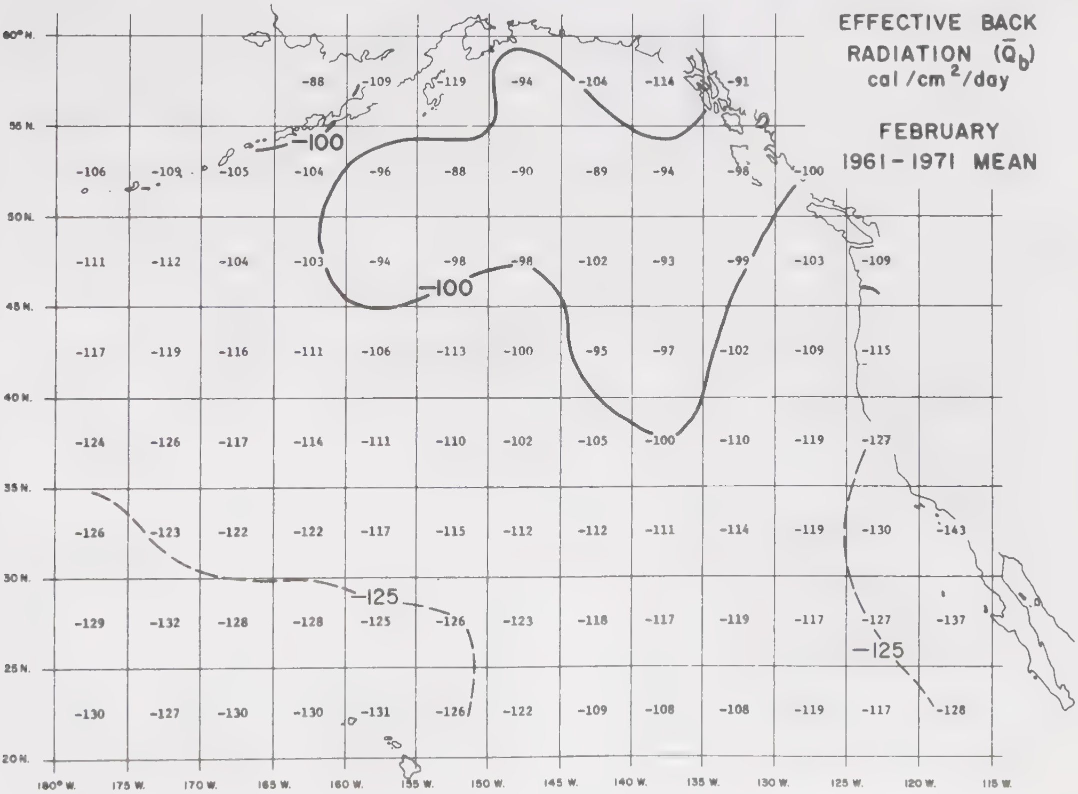
NET INCOMING RADIATION ($\bar{Q}_i$) cal /cm^2/day

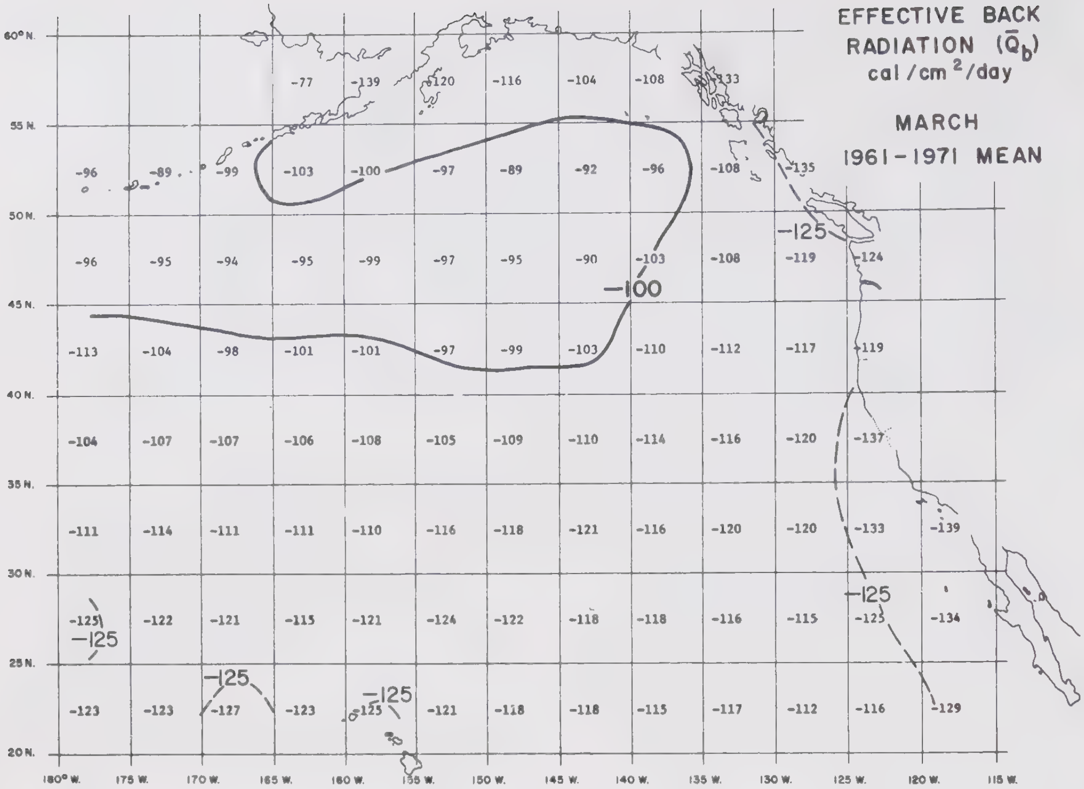
DECEMBER 1961-1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
24 21 25 23 21 22 22
+75
40 41 41 39 36 37 38 38 39 39 34
+50
67 65 68 66 62 63 64 65 63 65 64 69
98 99 102 93 93 95 91 96 93 98 103 113
+100
132 128 121 130 127 129 123 128 128 126 140 172
+150
179 176 168 173 181 179 175 172 168 170 177 206 232
+200
232 234 231 227 232 233 228 224 208 213 219 221 272
+250
+250
+275
288 297 291 295 289 279 282 266 254 229 207 210 261

PART 4. EFFECTIVE BACK RADIATION 1961-71 MEAN MONTHLY VALUES (NORMALS).

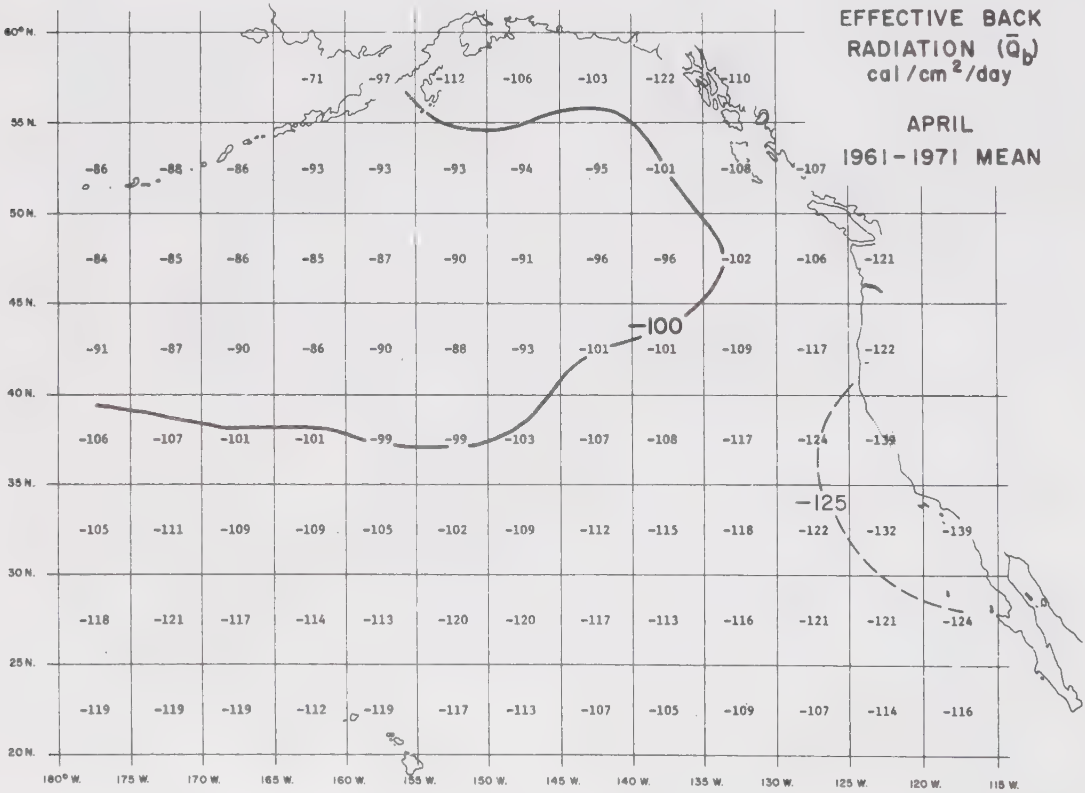

EFFECTIVE BACK
RADIATION ($\bar{Q}_b$)
cal/cm²/day
JANUARY
1961-1971 MEAN
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
-102 -141 -126 -116 -122 -142 -103
-125
-125
-104 -106 -113 -111 -107 -110 -98 -99 -104 -112 -94
-100
-100
-115 -108 -106 -100 -97 -98 -99 -99 -102 -106 -106 -117
-121 -122 -117 -118 -108 -102 -107 -102 -100 -107 -111 -120
-124 -123 -118 -119 -112 -108 -106 -105 -105 -110 -115 -136
-131 -126 -127 -126 -118 -114 -108 -108 -109 -117 -123 -133 -142
-125
-125
-133 -129 -132 -132 -127 -124 -117 -115 -113 -116 -121 -124 -139
-132 -132 -135 -129 -130 -120 -117 -112 -109 -109 -110 -122 -136
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W
125 W.
120 W.
115 W.


EFFECTIVE BACK
RADIATION ($\bar{Q}_b$)
cal/cm²/day
FEBRUARY
1961-1971 MEAN
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
-88 -109 -119 -94 -104 -114 -91
-100
-106 -109 -105 -104 -96 -88 -90 -89 -94 -98 -100
-111 -112 -104 -103 -94 -98 -98 -102 -93 -99 -103 -109
-100
-117 -119 -116 -111 -106 -113 -100 -95 -97 -102 -109 -115
-124 -126 -117 -114 -111 -110 -102 -105 -100 -110 -119 -127
-126 -123 -122 -122 -117 -115 -112 -112 -111 -114 -119 -130 -143
-125
-129 -132 -128 -128 -125 -126 -123 -118 -117 -119 -117 -127 -137
-125
-130 -127 -130 -130 -131 -126 -122 -109 -108 -108 -119 -117 -128
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


EFFECTIVE BACK
RADIATION ($\bar{Q}_b$)
cal/cm^2/day

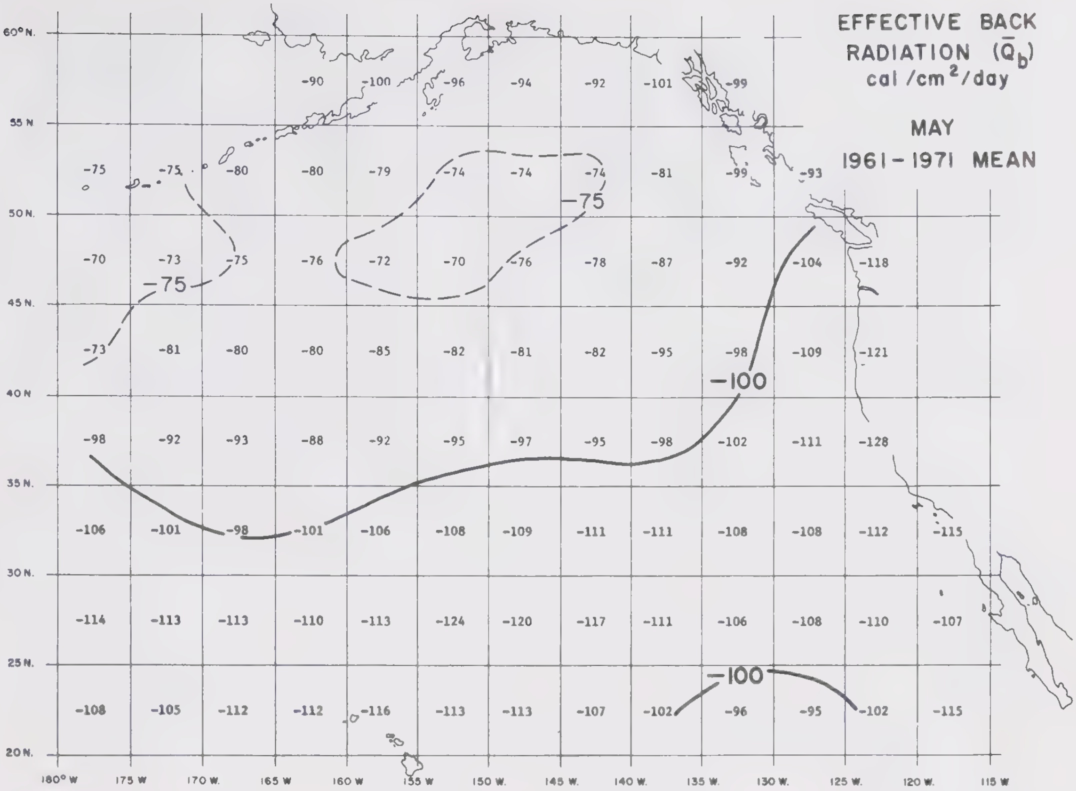
MARCH
1961-1971 MEAN

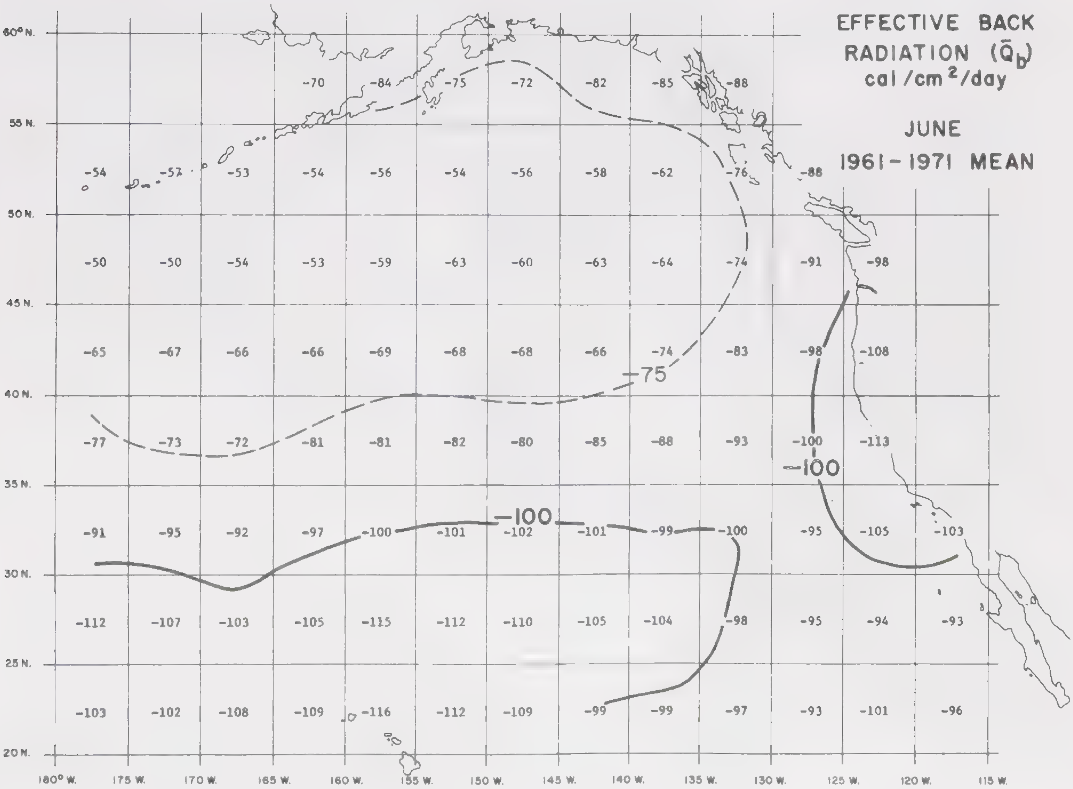
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-77 -139 -120 -116 -104 -108 -133
-96 -89 -99 -103 -100 -97 -89 -92 -96 -108 -135
-96 -95 -94 -95 -99 -97 -95 -90 -103 -108 -119 -124
-113 -104 -98 -101 -101 -97 -99 -103 -110 -112 -117 -119
-104 -107 -107 -106 -108 -105 -109 -110 -114 -116 -120 -137
-111 -114 -111 -111 -110 -116 -118 -121 -116 -120 -120 -133 -139
-125 -122 -121 -115 -121 -124 -122 -118 -118 -116 -115 -125 -134
-123 -123 -127 -123 -125 -121 -118 -118 -115 -117 -112 -116 -129
-100
-125
-125
-125
-125
-125

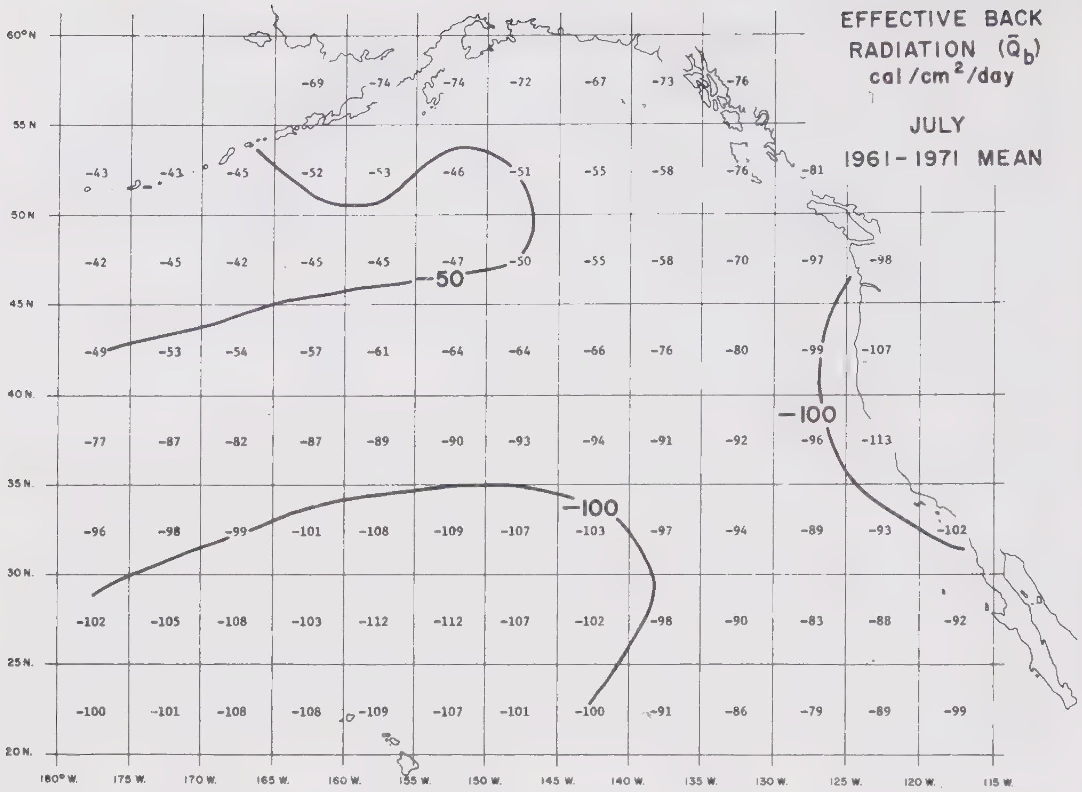

EFFECTIVE BACK
RADIATION ($\bar{Q}_b$)
cal/cm^2/day

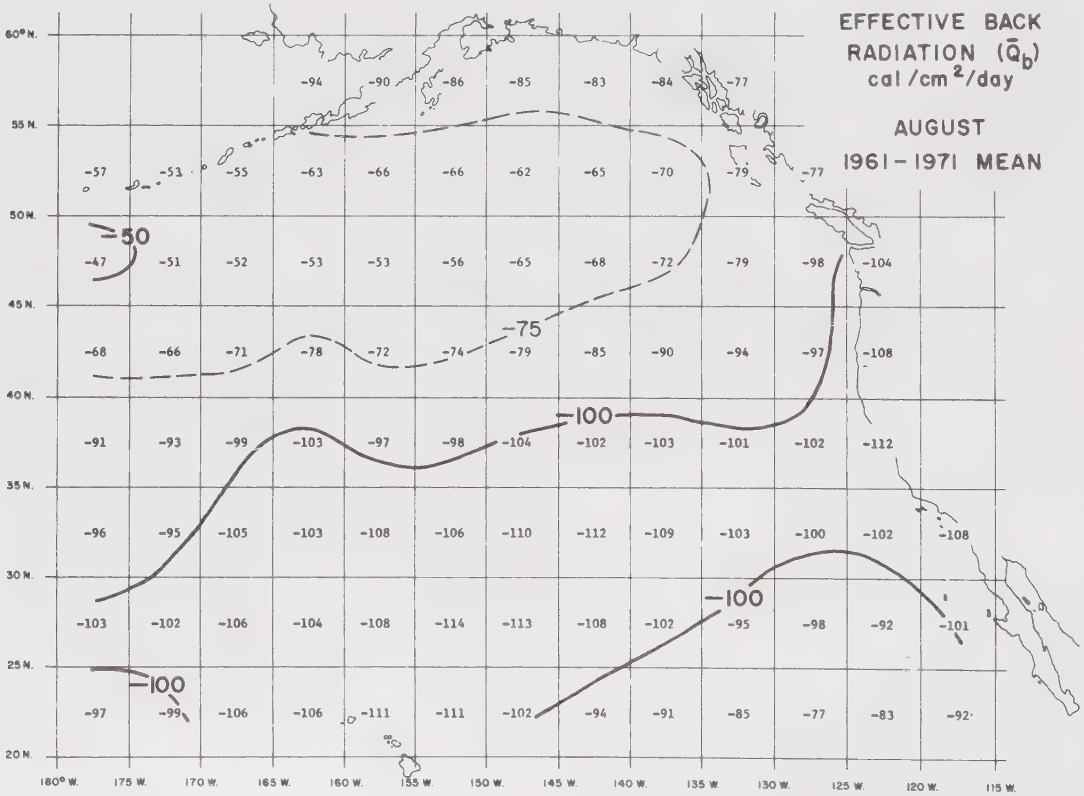
APRIL
1961-1971 MEAN

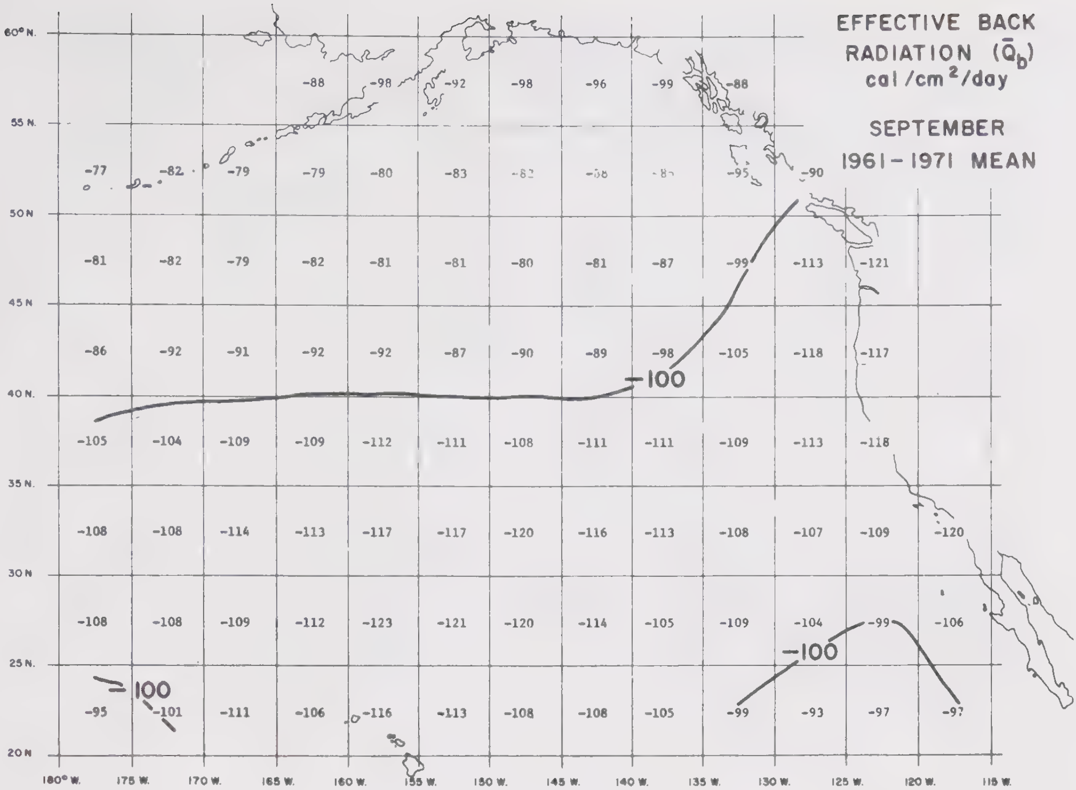
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-71 -97 -112 -106 -103 -122 -110
-86 -88 -86 -93 -93 -93 -94 -95 -101 -108 -107
-84 -85 -86 -85 -87 -90 -91 -96 -96 -102 -106 -121
-91 -87 -90 -86 -90 -88 -93 -101 -101 -109 -117 -122
-106 -107 -101 -101 -99 -99 -103 -107 -108 -117 -124 -139
-105 -111 -109 -109 -105 -102 -109 -112 -115 -118 -122 -132 -139
-118 -121 -117 -114 -113 -120 -120 -117 -113 -116 -121 -121 -124
-119 -119 -119 -112 -119 -117 -113 -107 -105 -109 -107 -114 -116
-100
-125


EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm²/day
MAY
1961 - 1971 MEAN
-90 -100 -96 -94 -92 -101 -99
-75 -75 -80 -80 -79 -74 -74 -74 -81 -99 -93
-70 -73 -75 -76 -72 -70 -76 -78 -87 -92 -104 -118
-73 -81 -80 -80 -85 -82 -81 -82 -95 -98 -109 -121
-98 -92 -93 -88 -92 -95 -97 -95 -98 -102 -111 -128
-106 -101 -98 -101 -106 -108 -109 -111 -111 -108 -108 -112 -115
-114 -113 -113 -110 -113 -124 -120 -117 -111 -106 -108 -110 -107
-108 -105 -112 -112 -116 -113 -113 -107 -102 -96 -95 -102 -115
-75
-75
-100
-100
60° N.
55 N
50 N.
45 N.
40 N
35 N.
30 N.
25 N.
20 N.
180° W
175 W
170 W.
165 W
160 W
155 W
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W


EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm²/day
JUNE
1961 - 1971 MEAN
-70 -84 -75 -72 -82 -85 -88
-54 -57 -53 -54 -56 -54 -56 -58 -62 -76 -88
-50 -50 -54 -53 -59 -63 -60 -63 -64 -74 -91 -98
-65 -67 -66 -66 -69 -68 -68 -66 -74 -83 -98 -108
-77 -73 -72 -81 -81 -82 -80 -85 -88 -93 -100 -113
-91 -95 -92 -97 -100 -101 -102 -101 -99 -100 -95 -105 -103
-112 -107 -103 -105 -115 -112 -110 -105 -104 -98 -95 -94 -93
-103 -102 -108 -109 -116 -112 -109 -99 -99 -97 -93 -101 -96
-75
-100
-100
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm^2/day
JULY
1961-1971 MEAN
-69
-74
-74
-72
-67
-73
-76
-43
-43
-45
-52
-53
-46
-51
-55
-58
-76
-81
-42
-45
-42
-45
-45
-47
-50
-55
-58
-70
-97
-98
-50
-49
-53
-54
-57
-61
-64
-64
-66
-76
-80
-99
-107
-100
-77
-87
-82
-87
-89
-90
-93
-94
-91
-92
-96
-113
-100
-96
-98
-99
-101
-108
-109
-107
-103
-97
-94
-89
-93
-102
-102
-105
-108
-103
-112
-112
-107
-102
-98
-90
-83
-88
-92
-100
-101
-108
-108
-109
-107
-101
-100
-91
-86
-79
-89
-99
60° N
55 N
50 N
45 N
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.

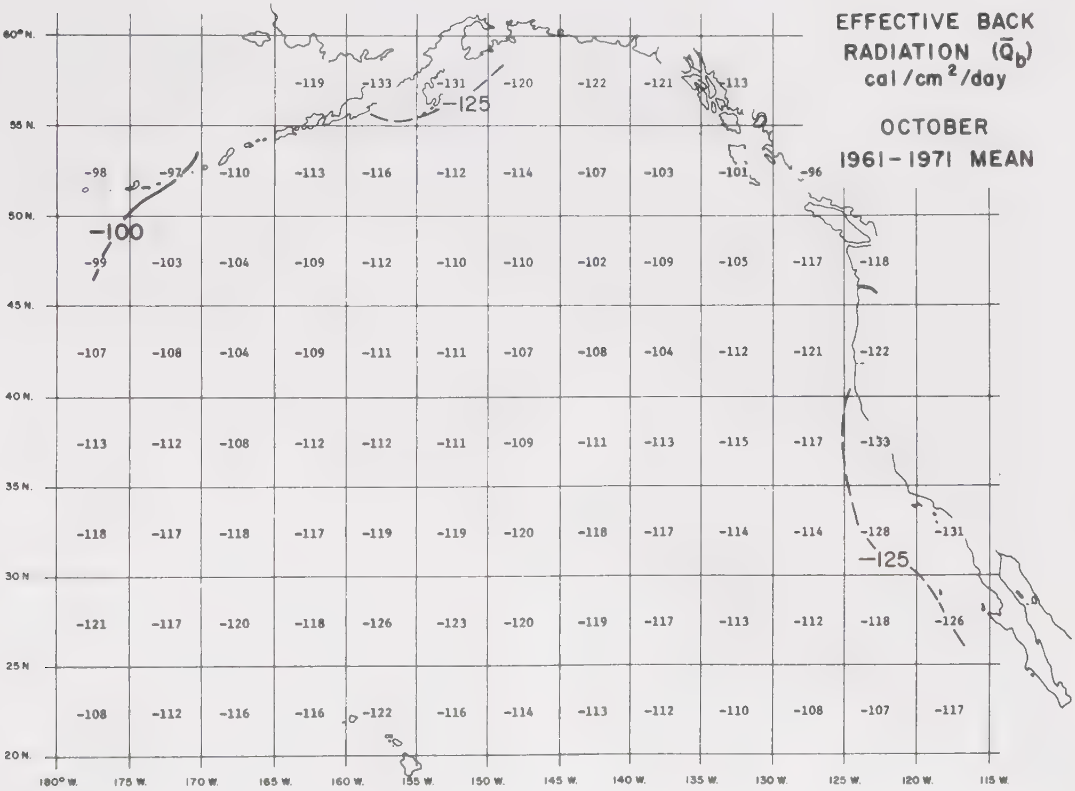

EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm^2/day
AUGUST
1961-1971 MEAN
-94
-90
-86
-85
-83
-84
-77
-57
-53
-55
-63
-66
-66
-62
-65
-70
-79
-77
-50
-47
-51
-52
-53
-53
-56
-65
-68
-72
-79
-98
-104
-75
-68
-66
-71
-78
-72
-74
-79
-85
-90
-94
-97
-108
-100
-91
-93
-99
-103
-97
-98
-104
-102
-103
-101
-102
-112
-96
-95
-105
-103
-108
-106
-110
-112
-109
-103
-100
-102
-108
-100
-103
-102
-106
-104
-108
-114
-113
-108
-102
-95
-98
-92
-101
-100
-97
-99
-106
-106
-111
-111
-102
-94
-91
-85
-77
-83
-92
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.



EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm^2/day

SEPTEMBER 1961-1971 MEAN

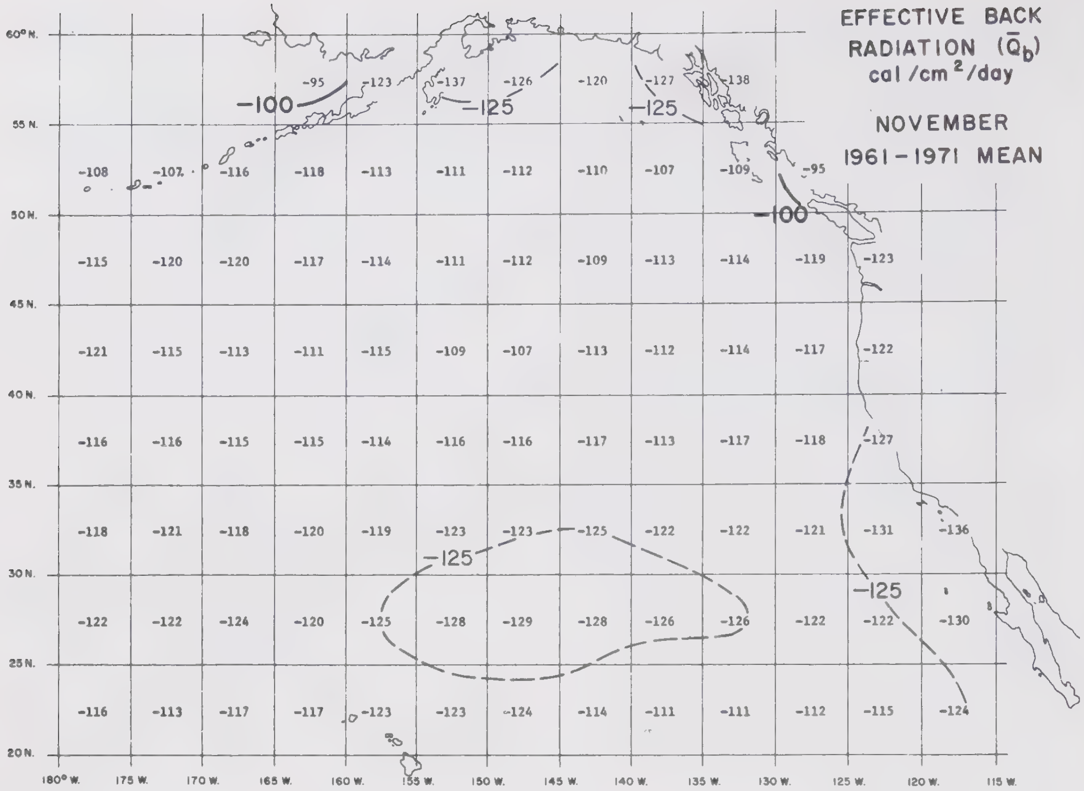
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-88 -98 -92 -98 -96 -99 -88
-77 -82 -79 -79 -80 -83 -82 -88 -87 -95 -90
-81 -82 -79 -82 -81 -81 -80 -81 -87 -99 -113 -121
-86 -92 -91 -92 -92 -87 -90 -89 -98 -105 -118 -117
-100
-105 -104 -109 -109 -112 -111 -108 -111 -111 -109 -113 -118
-108 -108 -114 -113 -117 -117 -120 -116 -113 -108 -107 -109 -120
-108 -108 -109 -112 -123 -121 -120 -114 -105 -109 -104 -99 -106
-100
100
-95 -101 -111 -106 -116 -113 -108 -108 -105 -99 -93 -97 -97



EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal/cm^2/day

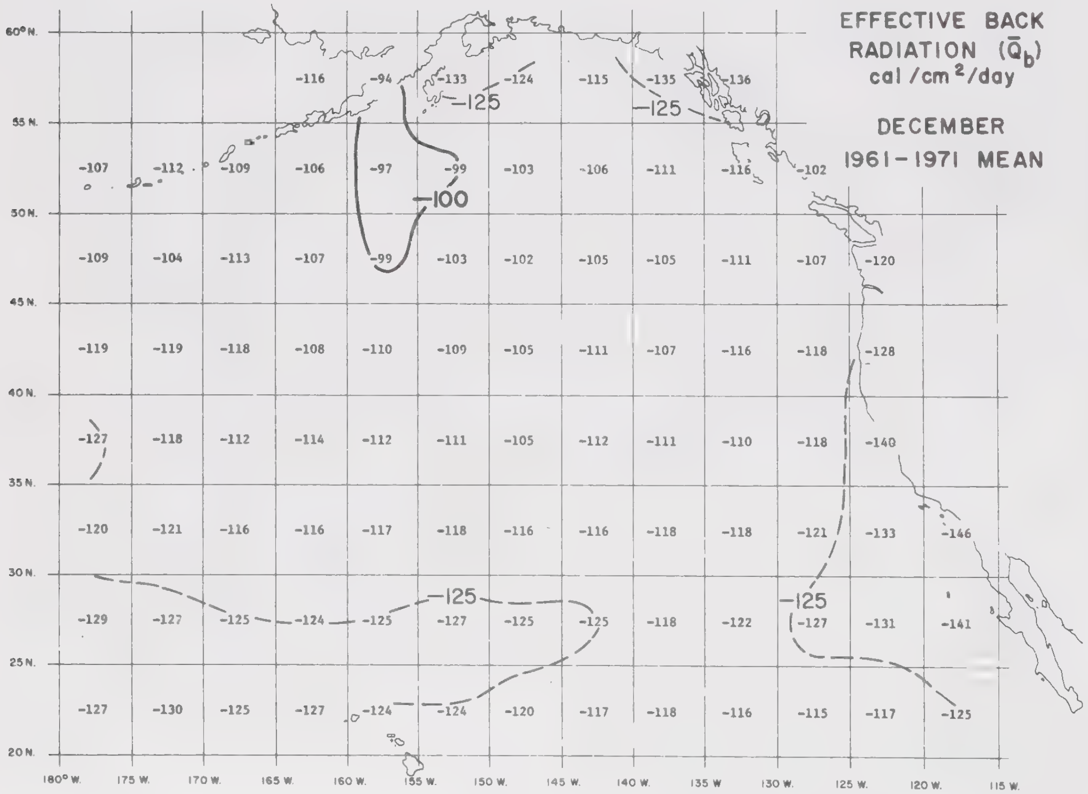
OCTOBER 1961-1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-119 -133 -131 -120 -122 -121 -113
-125
-98 -97 -110 -113 -116 -112 -114 -107 -103 -101 -96
-100
-99 -103 -104 -109 -112 -110 -110 -102 -109 -105 -117 -118
-107 -108 -104 -109 -111 -111 -107 -108 -104 -112 -121 -122
-113 -112 -108 -112 -112 -111 -109 -111 -113 -115 -117 -133
-118 -117 -118 -117 -119 -119 -120 -118 -117 -114 -114 -128 -131
-125
-121 -117 -120 -118 -126 -123 -120 -119 -117 -113 -112 -118 -126
-108 -112 -116 -116 -122 -116 -114 -113 -112 -110 -108 -107 -117


EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal /cm^2/day

NOVEMBER 1961-1971 MEAN

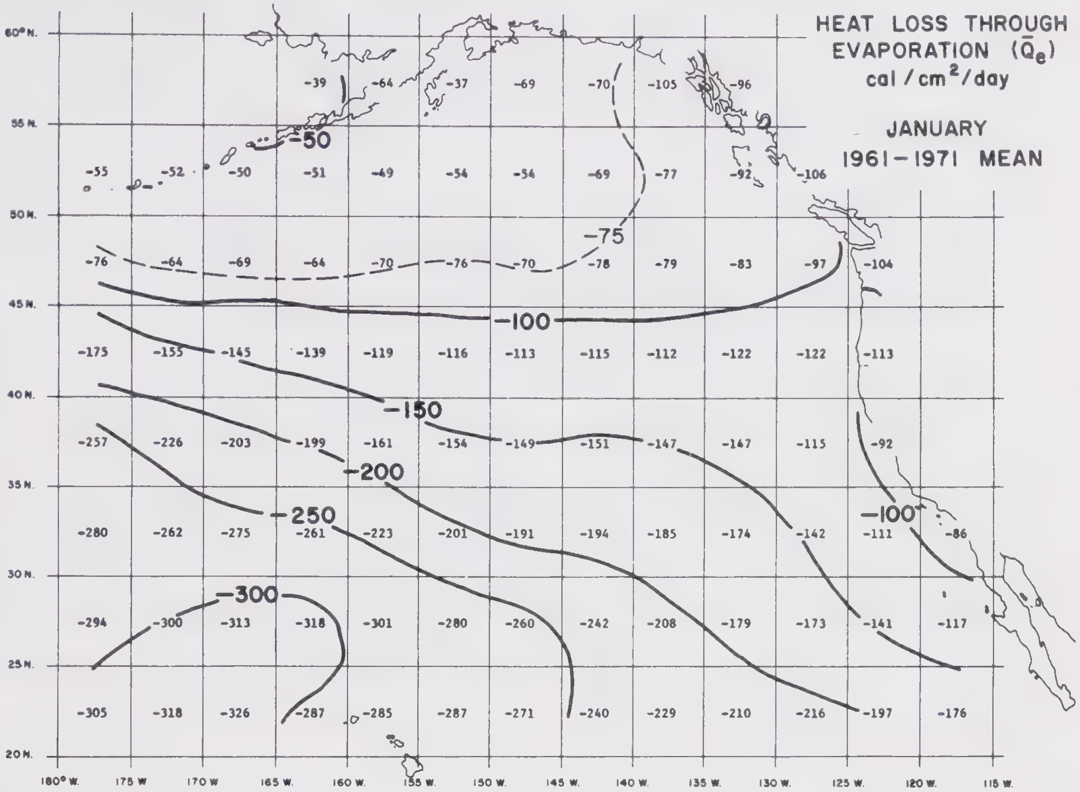
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-95 -123 -137 -126 -120 -127 -138
-100
-125
-125
-108 -107 -116 -118 -113 -111 -112 -110 -107 -109 -95
-100
-115 -120 -120 -117 -114 -111 -112 -109 -113 -114 -119 -123
-121 -115 -113 -111 -115 -109 -107 -113 -112 -114 -117 -122
-116 -116 -115 -115 -114 -116 -116 -117 -113 -117 -118 -127
-118 -121 -118 -120 -119 -123 -123 -125 -122 -122 -121 -131 -136
-125
-122 -122 -124 -120 -125 -128 -129 -128 -126 -126 -122 -122 -130
-125
-116 -113 -117 -117 -123 -123 -124 -114 -111 -111 -112 -115 -124

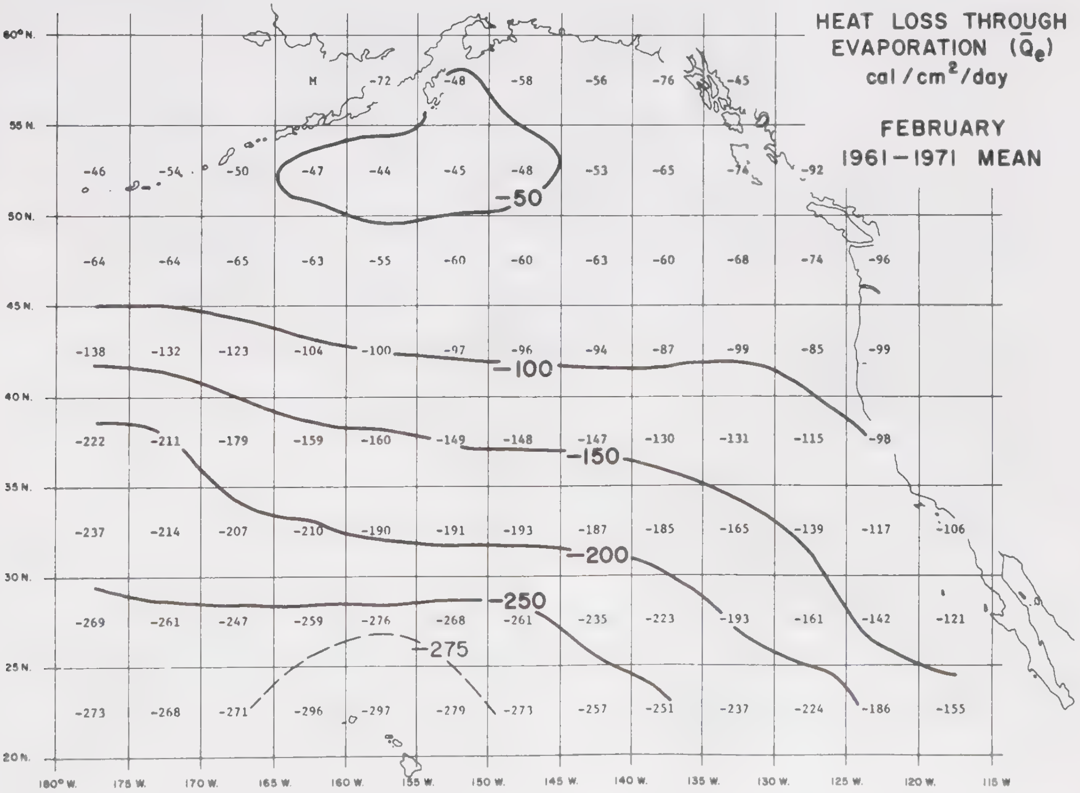

EFFECTIVE BACK RADIATION ($\bar{Q}_b$) cal /cm^2/day

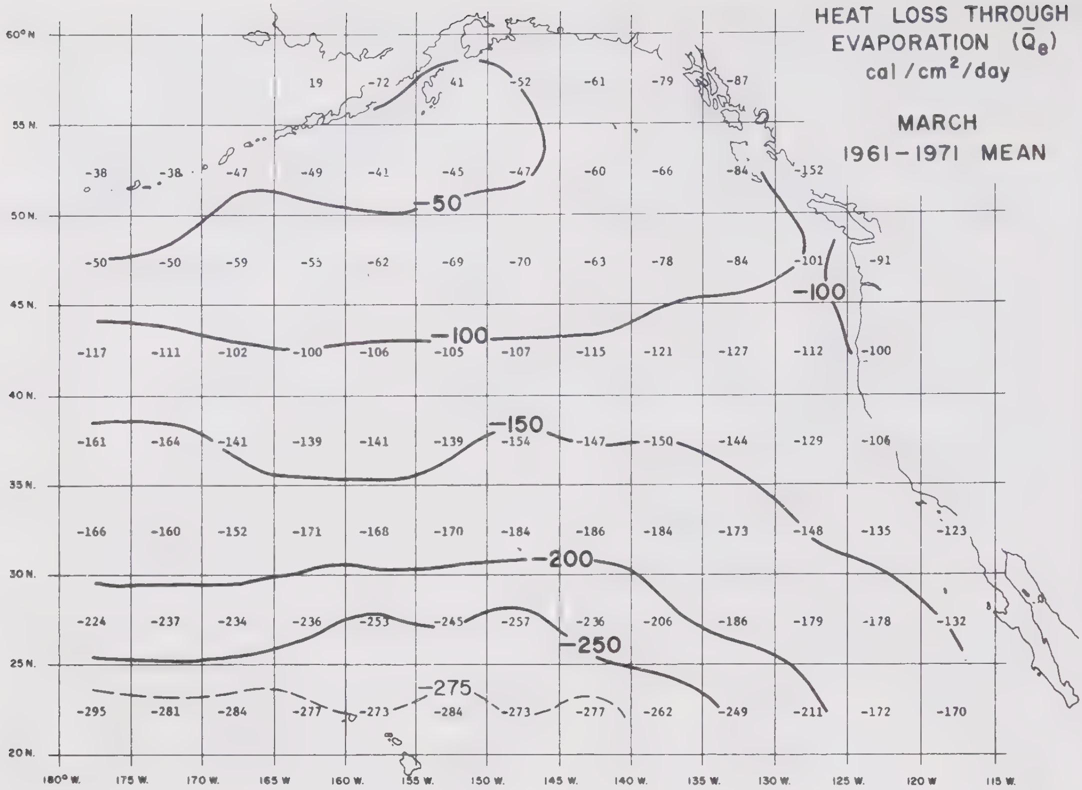
DECEMBER 1961-1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-116 -94 -133 -124 -115 -135 -136
-125
-125
-107 -112 -109 -106 -97 -99 -103 -106 -111 -116 -102
-100
-109 -104 -113 -107 -99 -103 -102 -105 -105 -111 -107 -120
-119 -119 -118 -108 -110 -109 -105 -111 -107 -116 -118 -128
-127 -118 -112 -114 -112 -111 -105 -112 -111 -110 -118 -140
-120 -121 -116 -116 -117 -118 -116 -116 -118 -118 -121 -133 -146
-125
-125
-129 -127 -125 -124 -125 -127 -125 -125 -118 -122 -127 -131 -141
-127 -130 -125 -127 -124 -124 -120 -117 -118 -116 -115 -117 -125

PART 5. EVAPORATIVE HEAT FLUX 1961-71 MEAN MONTHLY VALUES (NORMALS).


HEAT LOSS THROUGH
EVAPORATION ($\bar{Q}_e$)
cal / cm^2 / day
JANUARY
1961 – 1971 MEAN
-39 -64 -37 -69 -70 -105 -96
-50
-55 -52 -50 -51 -49 -54 -54 -69 -77 -92 -106
-75
-76 -64 -69 -64 -70 -76 -70 -78 -79 -83 -97 -104
-100
-175 -155 -145 -139 -119 -116 -113 -115 -112 -122 -122 -113
-150
-257 -226 -203 -199 -161 -154 -149 -151 -147 -147 -115 -92
-200
-250
-100
-280 -262 -275 -261 -223 -201 -191 -194 -185 -174 -142 -111 -86
-300
-294 -300 -313 -318 -301 -280 -260 -242 -208 -179 -173 -141 -117
-305 -318 -326 -287 -285 -287 -271 -240 -229 -210 -216 -197 -176
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W
170 W
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.


HEAT LOSS THROUGH
EVAPORATION ($\bar{Q}_e$)
cal / cm^2 / day
FEBRUARY
1961 – 1971 MEAN
M -72 -48 -58 -56 -76 -45
-46 -54 -50 -47 -44 -45 -48 -53 -65 -74 -92
-50
-64 -64 -65 -63 -55 -60 -60 -63 -60 -68 -74 -96
-138 -132 -123 -104 -100 -97 -96 -94 -87 -99 -85 -99
-100
-222 -211 -179 -159 -160 -149 -148 -147 -130 -131 -115 -98
-150
-237 -214 -207 -210 -190 -191 -193 -187 -185 -165 -139 -117 -106
-200
-250
-269 -261 -247 -259 -276 -268 -261 -235 -223 -193 -161 -142 -121
-275
-273 -268 -271 -296 -297 -279 -273 -257 -251 -237 -224 -186 -155
60°N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W

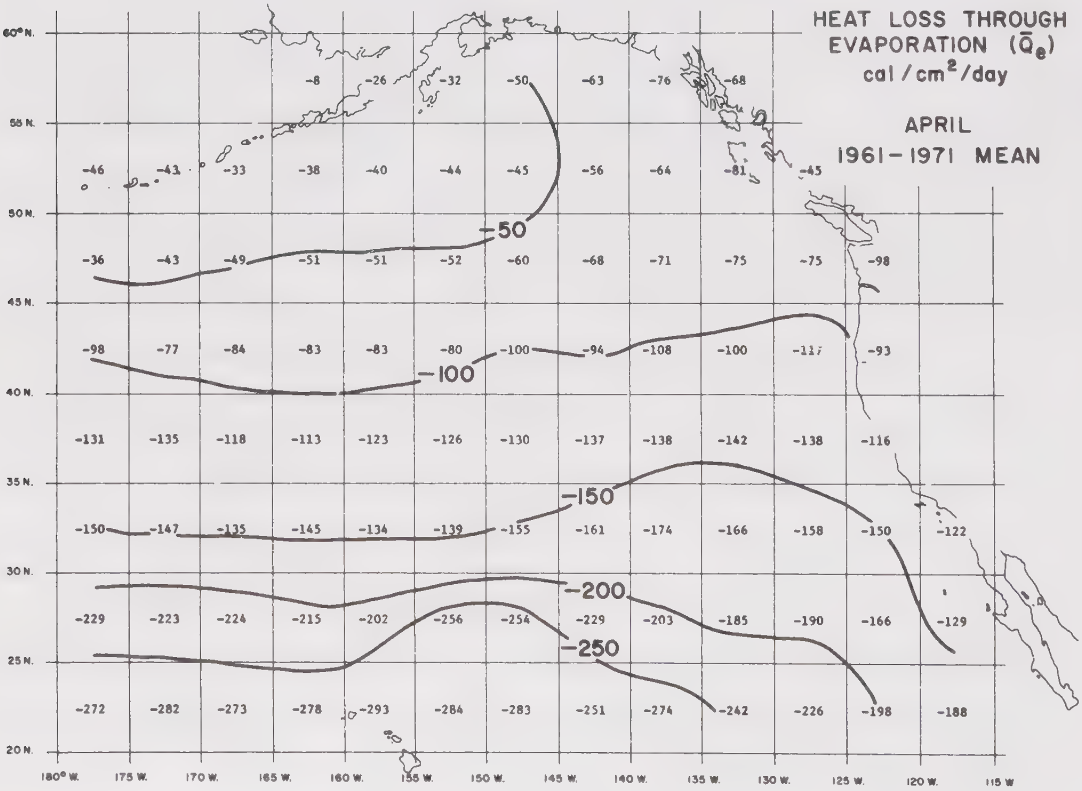


HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$) cal / cm^2 / day

MARCH

1961 – 1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
19 -72 41 -52 -61 -79 -87
-38 -38 -47 -49 -41 -45 -47 -60 -66 -84 -152
-50 -50 -59 -55 -62 -69 -70 -63 -78 -84 -101 -91
-117 -111 -102 -100 -106 -105 -107 -115 -121 -127 -112 -100
-161 -164 -141 -139 -141 -139 -154 -147 -150 -144 -129 -106
-166 -160 -152 -171 -168 -170 -184 -186 -184 -173 -148 -135 -123
-224 -237 -234 -236 -253 -245 -257 -236 -206 -186 -179 -178 -132
-295 -281 -284 -277 -273 -284 -273 -277 -262 -249 -211 -172 -170
-50
-100
-100
-150
-200
-250
-275

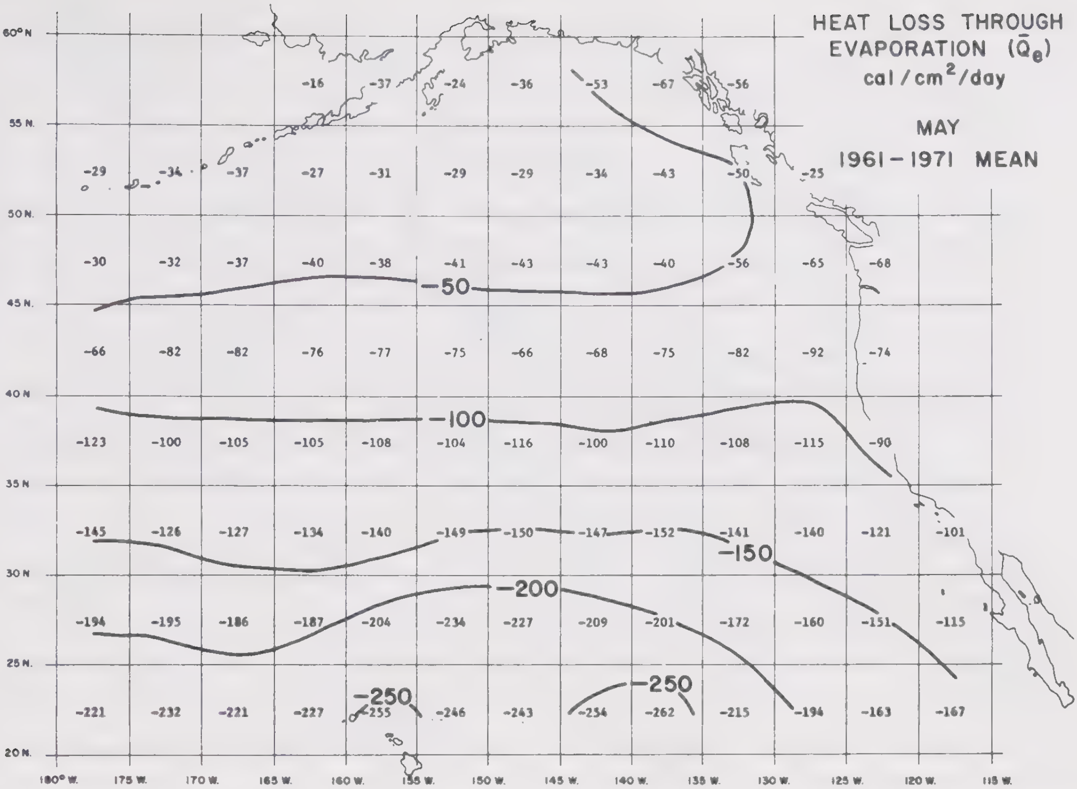


HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$) cal / cm^2 / day

APRIL

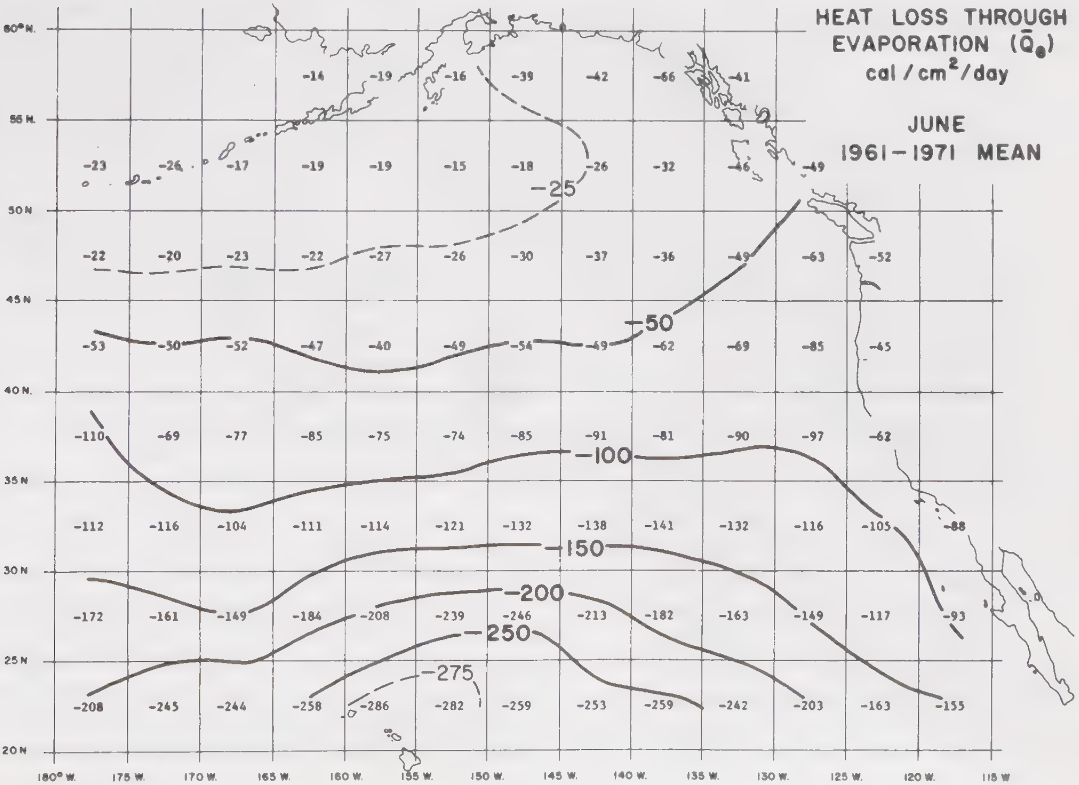
1961 – 1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-8 -26 -32 -50 -63 -76 -68
-46 -43 -33 -38 -40 -44 -45 -56 -64 -81 -45
-36 -43 -49 -51 -51 -52 -60 -68 -71 -75 -75 -98
-98 -77 -84 -83 -83 -80 -100 -94 -108 -100 -117 -93
-131 -135 -118 -113 -123 -126 -130 -137 -138 -142 -138 -116
-150 -147 -135 -145 -134 -139 -155 -161 -174 -166 -158 -150 -122
-229 -223 -224 -215 -202 -256 -254 -229 -203 -185 -190 -166 -129
-272 -282 -273 -278 -293 -284 -283 -251 -274 -242 -226 -198 -188
-50
-100
-150
-200
-250


HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$)
cal / cm^2/day

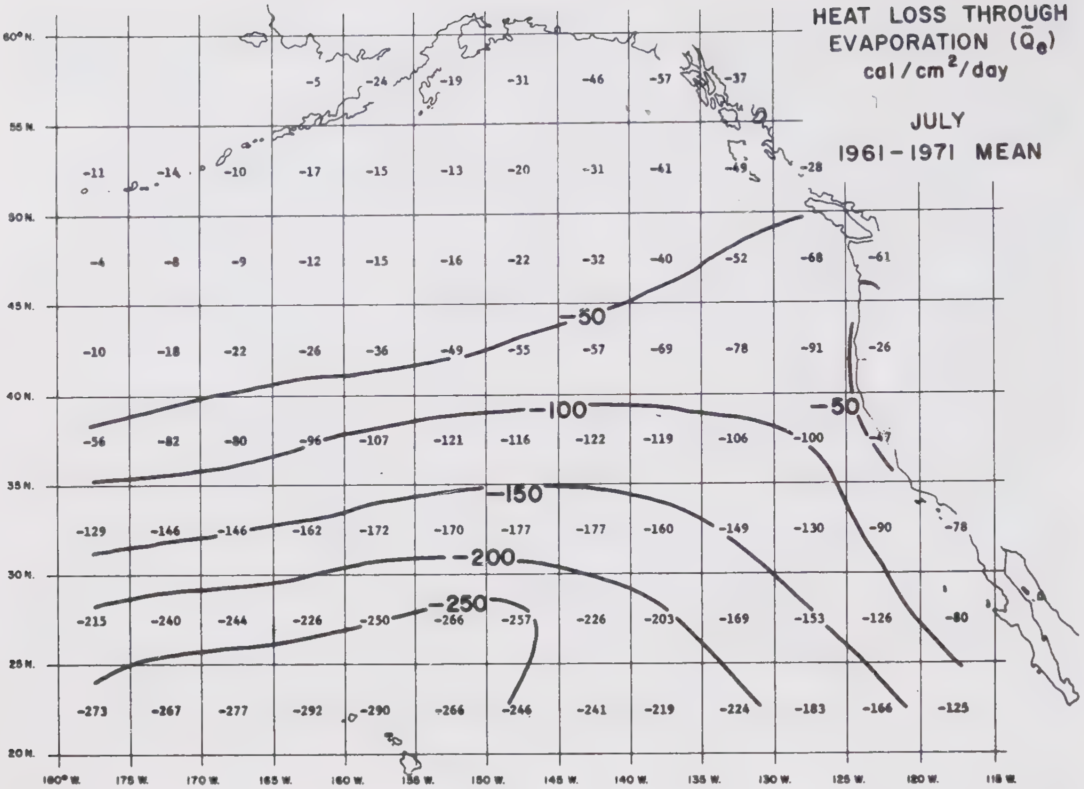
MAY
1961 – 1971 MEAN

60° N
55 N.
50 N.
45 N.
40 N
35 N
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-16 -37 -24 -36 -53 -67 -56
-29 -34 -37 -27 -31 -29 -29 -34 -43 -50 -25
-30 -32 -37 -40 -38 -41 -43 -43 -40 -56 -65 -68
-50
-66 -82 -82 -76 -77 -75 -66 -68 -75 -82 -92 -74
-100
-123 -100 -105 -105 -108 -104 -116 -100 -110 -108 -115 -90
-145 -126 -127 -134 -140 -149 -150 -147 -152 -141 -140 -121 -101
-150
-200
-194 -195 -186 -187 -204 -234 -227 -209 -201 -172 -160 -151 -115
-250
-250
-221 -232 -221 -227 -255 -246 -243 -254 -262 -215 -194 -163 -167


HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$)
cal / cm^2/day

JUNE
1961 – 1971 MEAN

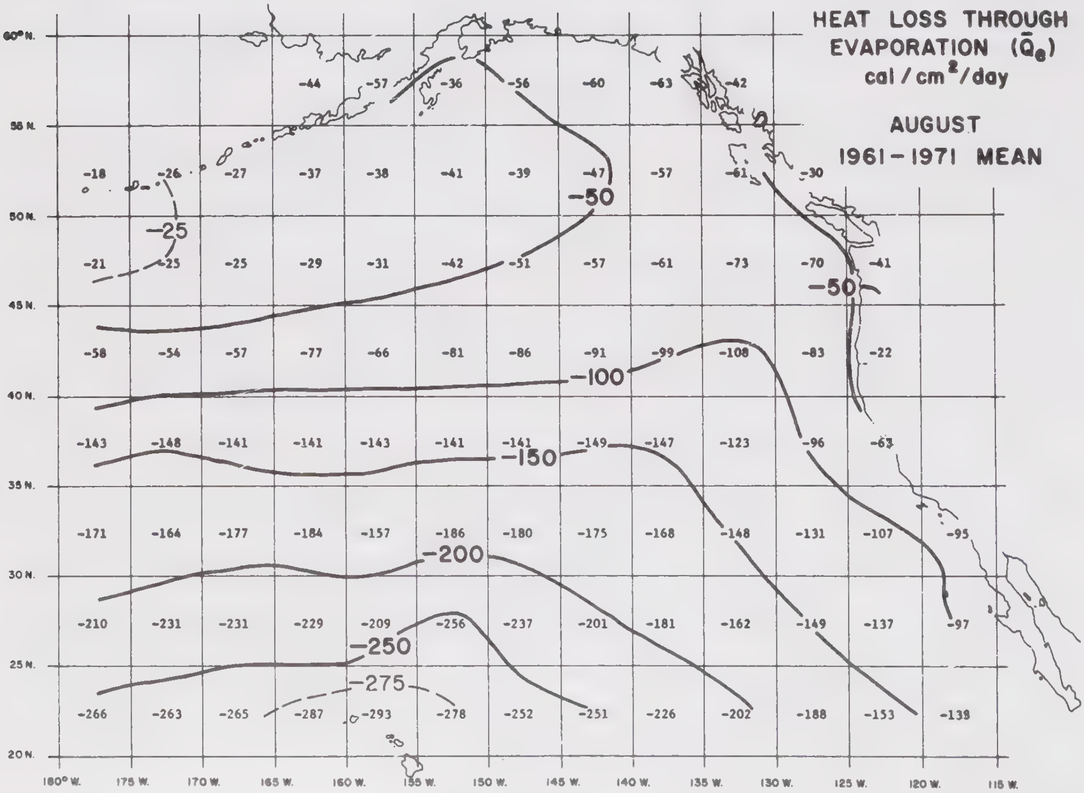
60° N.
55 N.
50 N
45 N
40 N.
35 N
30 N
25 N
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W
-14 -19 -16 -39 -42 -66 -41
-23 -26 -17 -19 -19 -15 -18 -26 -32 -46 -49
-25
-22 -20 -23 -22 -27 -26 -30 -37 -36 -49 -63 -52
-50
-53 -50 -52 -47 -40 -49 -54 -49 -62 -69 -85 -45
-110 -69 -77 -85 -75 -74 -85 -91 -81 -90 -97 -62
-100
-112 -116 -104 -111 -114 -121 -132 -138 -141 -132 -116 -105 -88
-150
-200
-172 -161 -149 -184 -208 -239 -246 -213 -182 -163 -149 -117 -93
-250
-275
-208 -245 -244 -258 -286 -282 -259 -253 -259 -242 -203 -163 -155



HEAT LOSS THROUGH EVAPORATION $(\bar{Q}_e)$
cal / cm^2/ day

JULY
1961 – 1971 MEAN

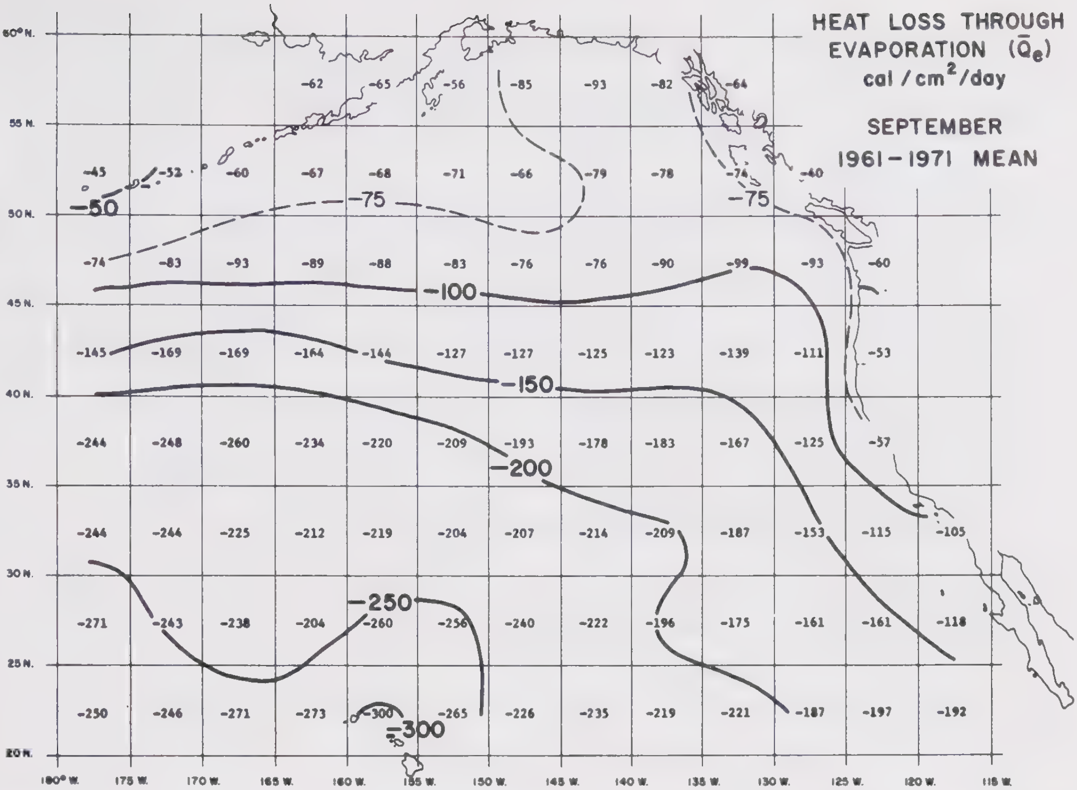
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-5 -24 -19 -31 -46 -57 -37
-11 -14 -10 -17 -15 -13 -20 -31 -41 -49 -28
-4 -8 -9 -12 -15 -16 -22 -32 -40 -52 -68 -61
-10 -18 -22 -26 -36 -49 -55 -57 -69 -78 -91 -26
-56 -82 -80 -96 -107 -121 -116 -122 -119 -106 -100 -47
-129 -146 -146 -162 -172 -170 -177 -177 -160 -149 -130 -90 -78
-215 -240 -244 -226 -250 -266 -257 -226 -203 -169 -153 -126 -80
-273 -267 -277 -292 -290 -266 -246 -241 -219 -224 -183 -166 -125
-50
-50
-100
-150
-200
-250



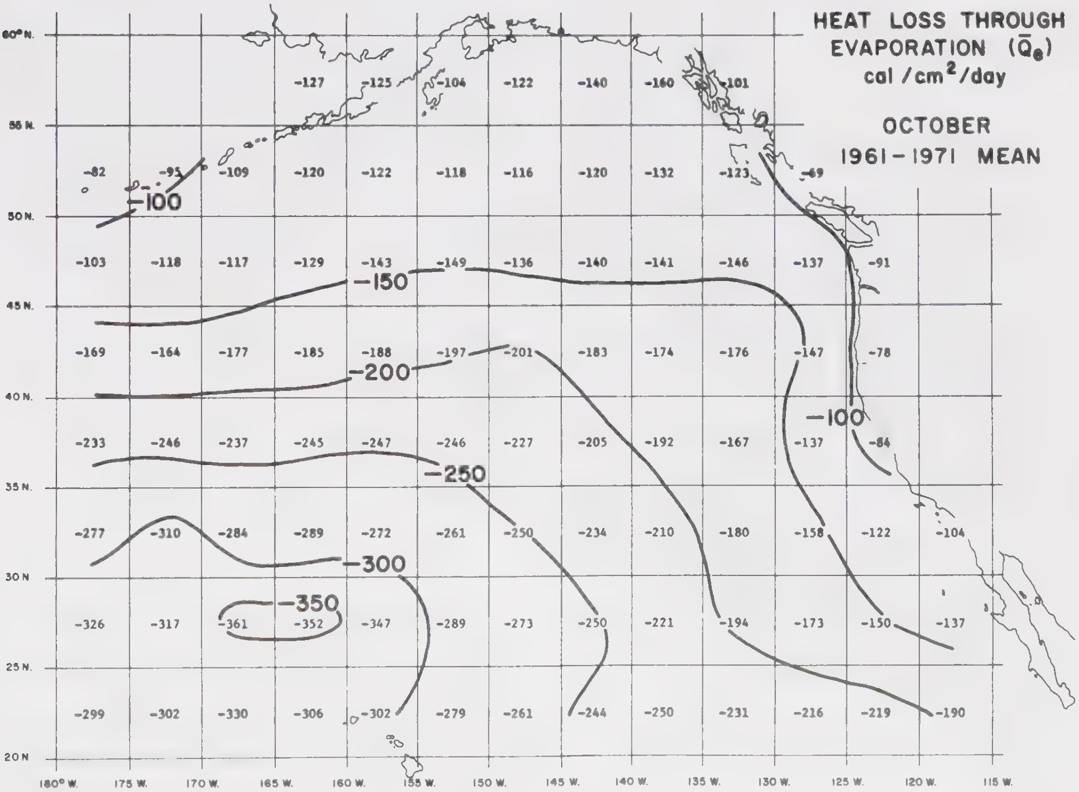
HEAT LOSS THROUGH EVAPORATION $(\bar{Q}_e)$
cal / cm^2/ day

AUGUST
1961 – 1971 MEAN

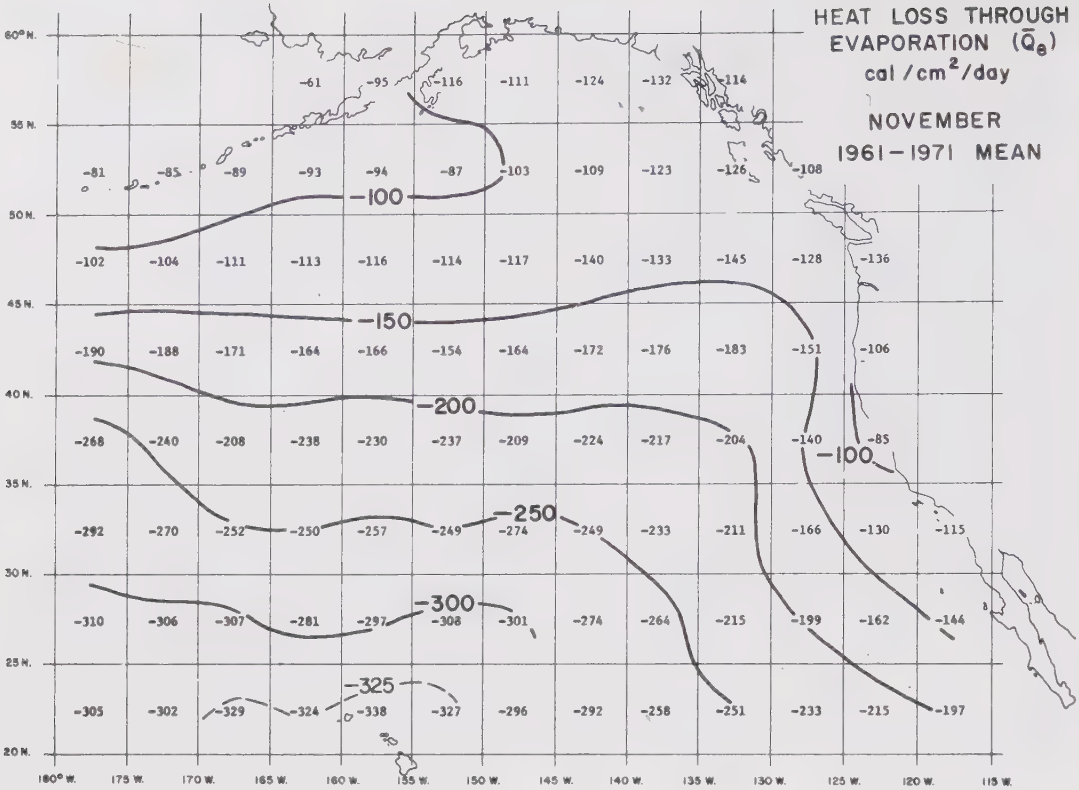
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-44 -57 -36 -56 -60 -63 -42
-18 -26 -27 -37 -38 -41 -39 -47 -57 -61 -30
-21 -25 -25 -29 -31 -42 -51 -57 -61 -73 -70 -41
-58 -54 -57 -77 -66 -81 -86 -91 -99 -108 -83 -22
-143 -148 -141 -141 -143 -141 -141 -149 -147 -123 -96 -63
-171 -164 -177 -184 -157 -186 -180 -175 -168 -148 -131 -107 -95
-210 -231 -231 -229 -209 -256 -237 -201 -181 -162 -149 -137 -97
-266 -263 -265 -287 -293 -278 -252 -251 -226 -202 -188 -153 -138
-25
-50
-50
-100
-150
-200
-250
-275



HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$)
cal / cm^2/day
SEPTEMBER
1961 – 1971 MEAN
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-62 -65 -56 -85 -93 -82 -64
-45 -52 -60 -67 -68 -71 -66 -79 -78 -74 -40
-50
-75
-75
-74 -83 -93 -89 -88 -83 -76 -76 -90 -99 -93 -60
-100
-145 -169 -169 -164 -144 -127 -127 -125 -123 -139 -111 -53
-150
-244 -248 -260 -234 -220 -209 -193 -178 -183 -167 -125 -57
-200
-244 -244 -225 -212 -219 -204 -207 -214 -209 -187 -153 -115 -105
-250
-271 -263 -238 -204 -260 -256 -240 -222 -196 -175 -161 -161 -118
-250 -246 -271 -273 -300 -265 -226 -235 -219 -221 -187 -197 -192
-300



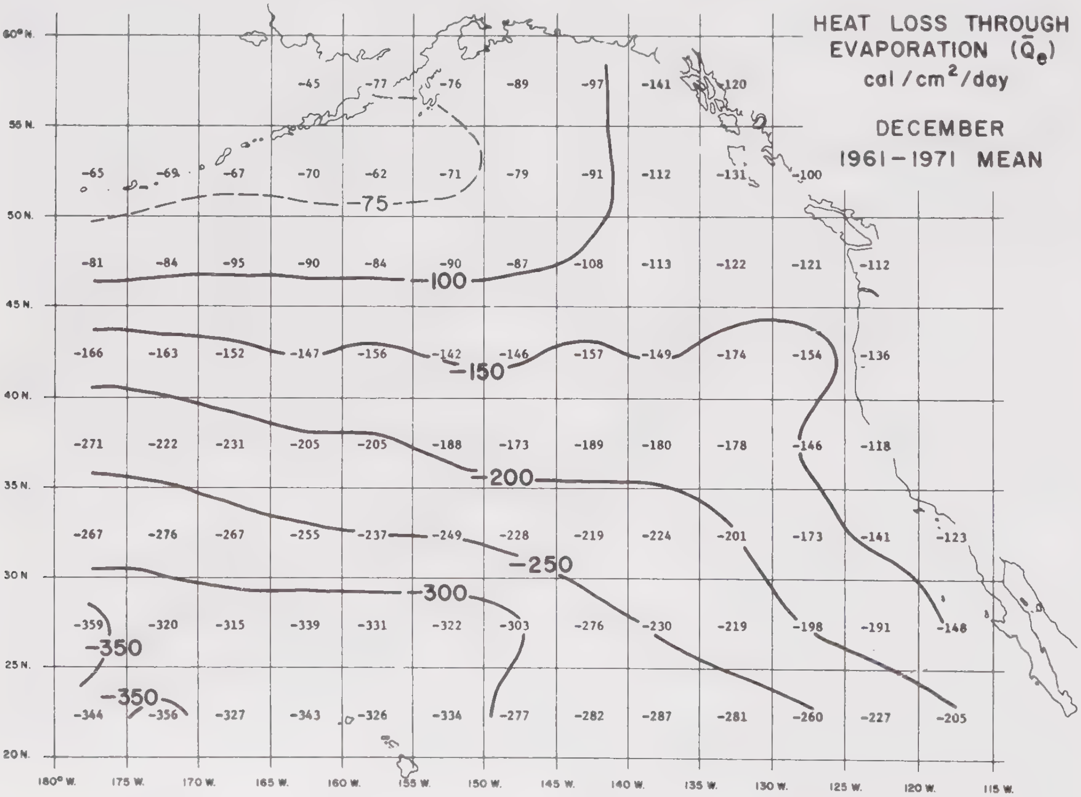
HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$)
cal / cm^2/day
OCTOBER
1961 – 1971 MEAN
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-127 -125 -104 -122 -140 -160 -101
-82 -95 -109 -120 -122 -118 -116 -120 -132 -123 -69
-100
-103 -118 -117 -129 -143 -149 -136 -140 -141 -146 -137 -91
-150
-169 -164 -177 -185 -188 -197 -201 -183 -174 -176 -147 -78
-200
-100
-233 -246 -237 -245 -247 -246 -227 -205 -192 -167 -137 -84
-250
-277 -310 -284 -289 -272 -261 -250 -234 -210 -180 -158 -122 -104
-300
-350
-326 -317 -361 -352 -347 -289 -273 -250 -221 -194 -173 -150 -137
-299 -302 -330 -306 -302 -279 -261 -244 -250 -231 -216 -219 -190



HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$) cal /cm^2/day

NOVEMBER 1961–1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N.
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-61 -95 -116 -111 -124 -132 -114
-81 -85 -89 -93 -94 -87 -103 -109 -123 -126 -108
-100
-102 -104 -111 -113 -116 -114 -117 -140 -133 -145 -128 -136
-150
-190 -188 -171 -164 -166 -154 -164 -172 -176 -183 -151 -106
-200
-268 -240 -208 -238 -230 -237 -209 -224 -217 -204 -140 -85
-100
-250
-292 -270 -252 -250 -257 -249 -274 -249 -233 -211 -166 -130 -115
-300
-310 -306 -307 -281 -297 -308 -301 -274 -264 -215 -199 -162 -144
-325
-305 -302 -329 -324 -338 -327 -296 -292 -258 -251 -233 -215 -197

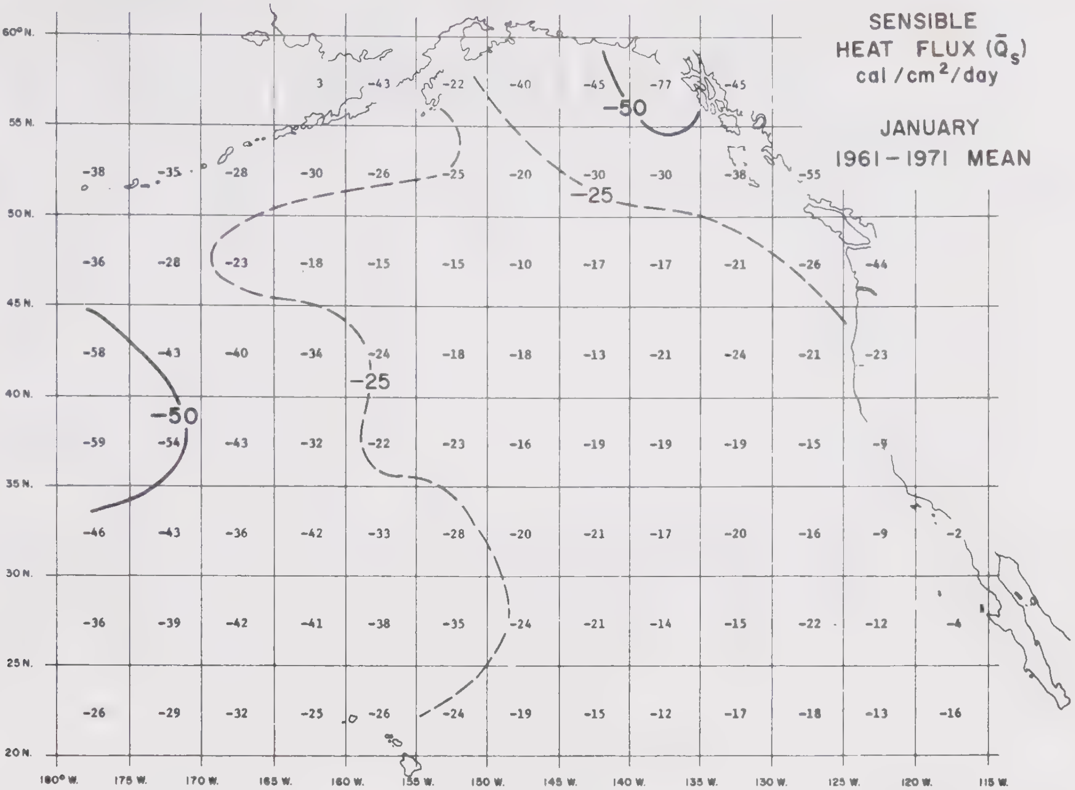


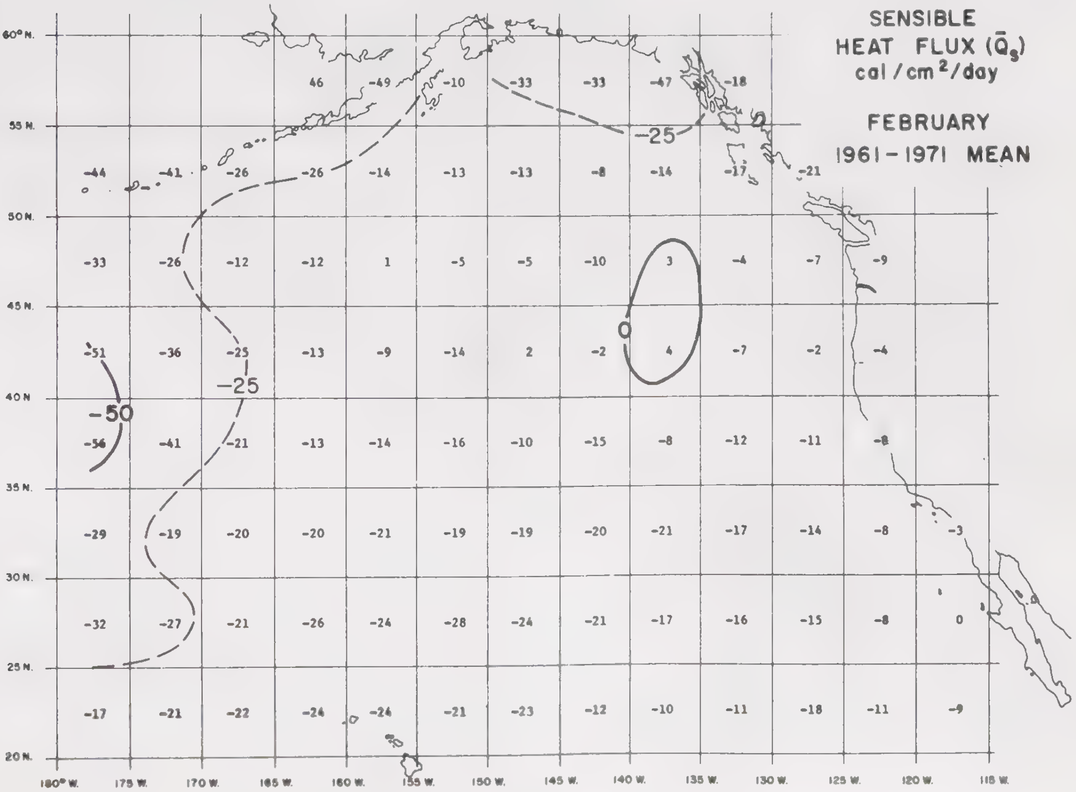
HEAT LOSS THROUGH EVAPORATION ($\bar{Q}_e$) cal /cm^2/day

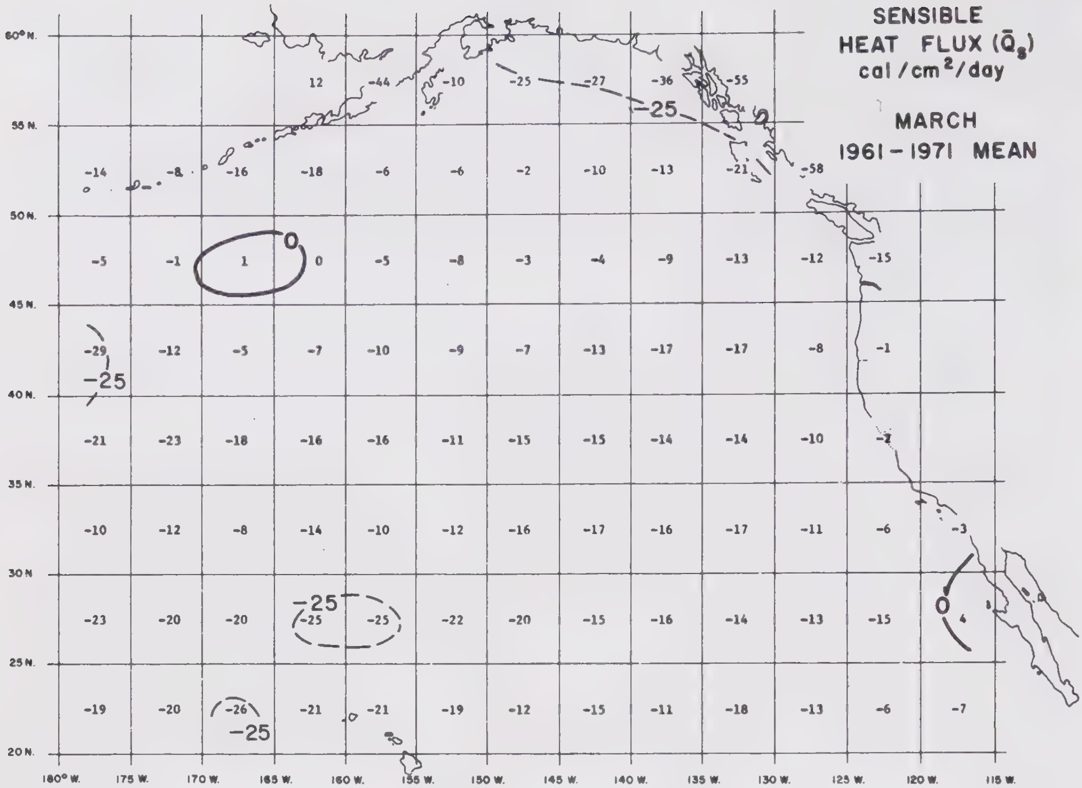
DECEMBER 1961–1971 MEAN

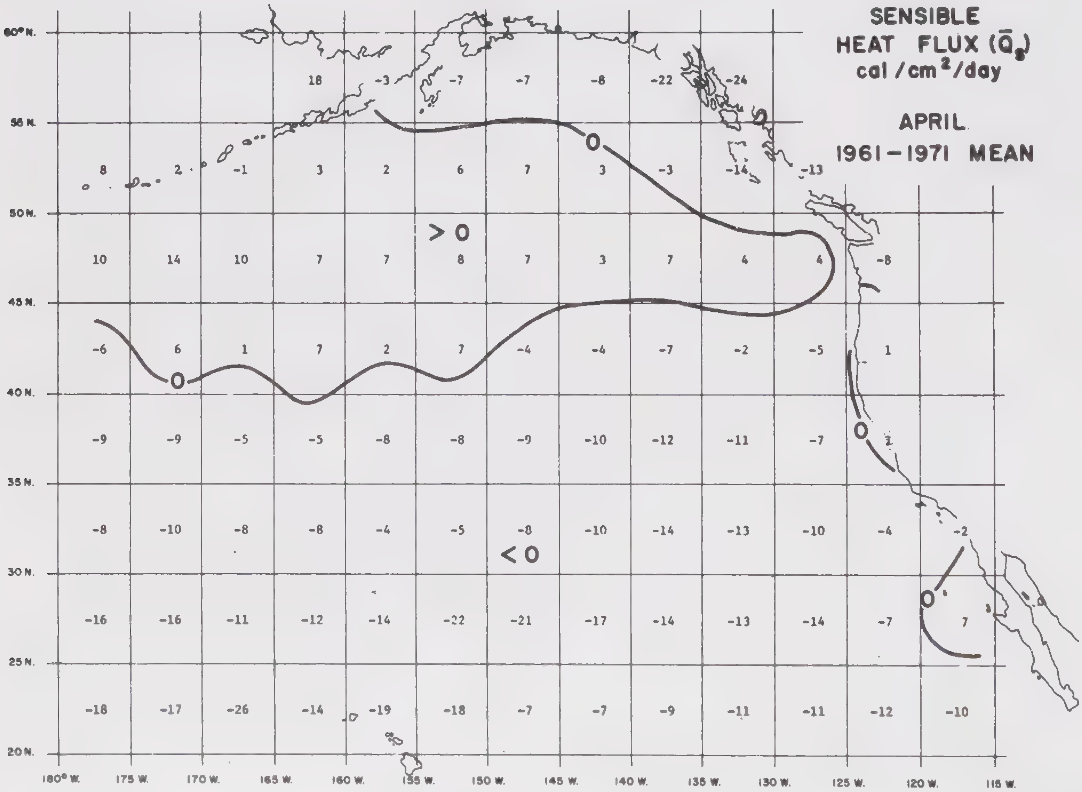
60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
-45 -77 -76 -89 -97 -141 -120
-65 -69 -67 -70 -62 -71 -79 -91 -112 -131 -100
-75
-81 -84 -95 -90 -84 -90 -87 -108 -113 -122 -121 -112
-100
-166 -163 -152 -147 -156 -142 -146 -157 -149 -174 -154 -136
-150
-271 -222 -231 -205 -205 -188 -173 -189 -180 -178 -146 -118
-200
-267 -276 -267 -255 -237 -249 -228 -219 -224 -201 -173 -141 -123
-250
-300
-359 -320 -315 -339 -331 -322 -303 -276 -230 -219 -198 -191 -148
-350
-350
-344 -356 -327 -343 -326 -334 -277 -282 -287 -281 -260 -227 -205

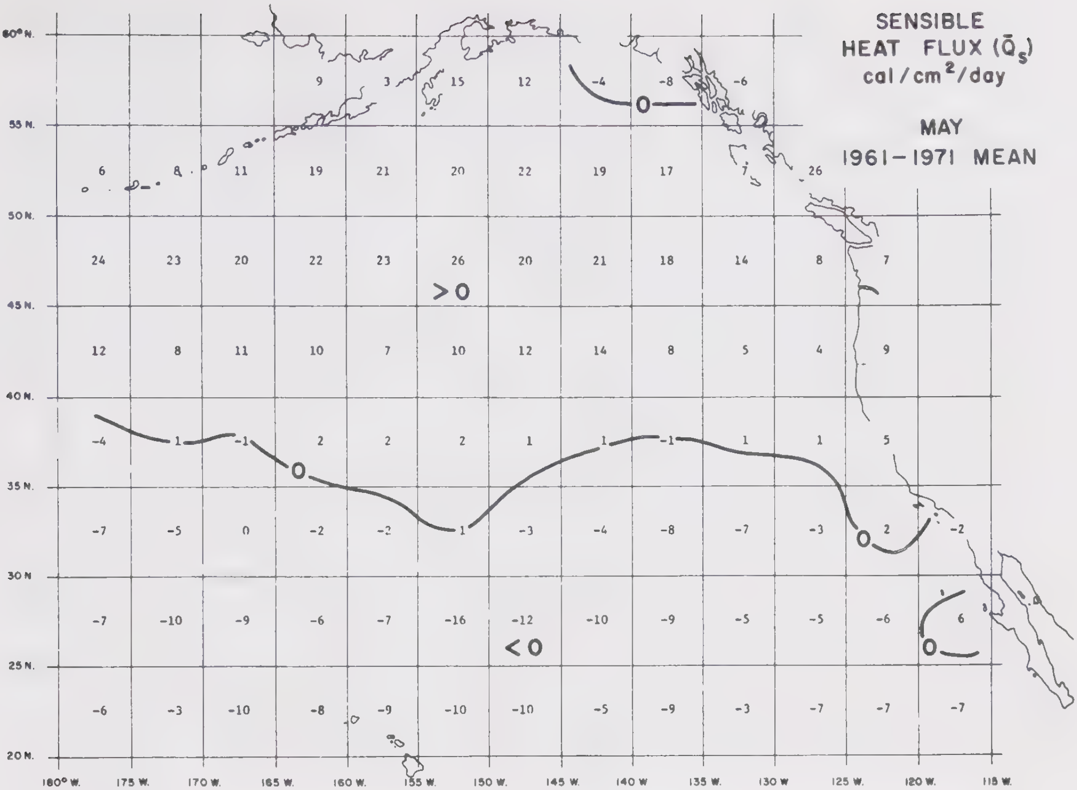
PART 6. SENSIBLE HEAT FLUX 1961-71 MEAN MONTHLY VALUES (NORMALS).


SENSIBLE
HEAT FLUX ($\bar{Q}_s$)
cal / cm^2/ day
JANUARY
1961 - 1971 MEAN
60°N.
55N.
50N.
45N.
40N.
35N.
30N.
25N.
20N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
3 -43 -22 -40 -45 -77 -45
-50
-38 -35 -28 -30 -26 -25 -20 -30 -30 -38 -55
-25
-36 -28 -23 -18 -15 -15 -10 -17 -17 -21 -26 -44
-58 -43 -40 -34 -24 -18 -18 -13 -21 -24 -21 -23
-25
-50
-59 -54 -43 -32 -22 -23 -16 -19 -19 -19 -15 -9
-46 -43 -36 -42 -33 -28 -20 -21 -17 -20 -16 -9 -2
-36 -39 -42 -41 -38 -35 -24 -21 -14 -15 -22 -12 -4
-26 -29 -32 -25 -26 -24 -19 -15 -12 -17 -18 -13 -16


SENSIBLE
HEAT FLUX ($\bar{Q}_s$)
cal / cm^2/ day
FEBRUARY
1961 - 1971 MEAN
60°N.
55N.
50N.
45N.
40N.
35N.
30N.
25N.
20N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W.
135 W.
130 W.
125 W.
120 W.
115 W.
46 -49 -10 -33 -33 -47 -18
-25
-44 -41 -26 -26 -14 -13 -13 -8 -14 -17 -21
-33 -26 -12 -12 1 -5 -5 -10 3 -4 -7 -9
-51 -36 -25 -13 -9 -14 2 -2 4 -7 -2 -4
0
-25
-50
-56 -41 -21 -13 -14 -16 -10 -15 -8 -12 -11 -8
-29 -19 -20 -20 -21 -19 -19 -20 -21 -17 -14 -8 -3
-32 -27 -21 -26 -24 -28 -24 -21 -17 -16 -15 -8 0
-17 -21 -22 -24 -24 -21 -23 -12 -10 -11 -18 -11 -9


SENSIBLE HEAT FLUX ($\bar{Q}_s$)
cal / cm² / day
MARCH
1961 - 1971 MEAN
12 -44 -10 -25 -27 -36 -55
-25
-14 -8 -16 -18 -6 -6 -2 -10 -13 -21 -58
0
-5 -1 1 0 -5 -8 -3 -4 -9 -13 -12 -15
-29 -12 -5 -7 -10 -9 -7 -13 -17 -17 -8 -1
-25
-21 -23 -18 -16 -16 -11 -15 -15 -14 -14 -10 -7
-10 -12 -8 -14 -10 -12 -16 -17 -16 -17 -11 -6 -3
-25
-23 -20 -20 -25 -25 -22 -20 -15 -16 -14 -13 -15 0 4
-19 -20 -26 -21 -21 -19 -12 -15 -11 -18 -13 -6 -7
-25
60° N. 55 N. 50 N. 45 N. 40 N. 35 N. 30 N. 25 N. 20 N.
180° W. 175 W. 170 W. 165 W. 160 W. 155 W. 150 W. 145 W. 140 W. 135 W. 130 W. 125 W. 120 W. 115 W.

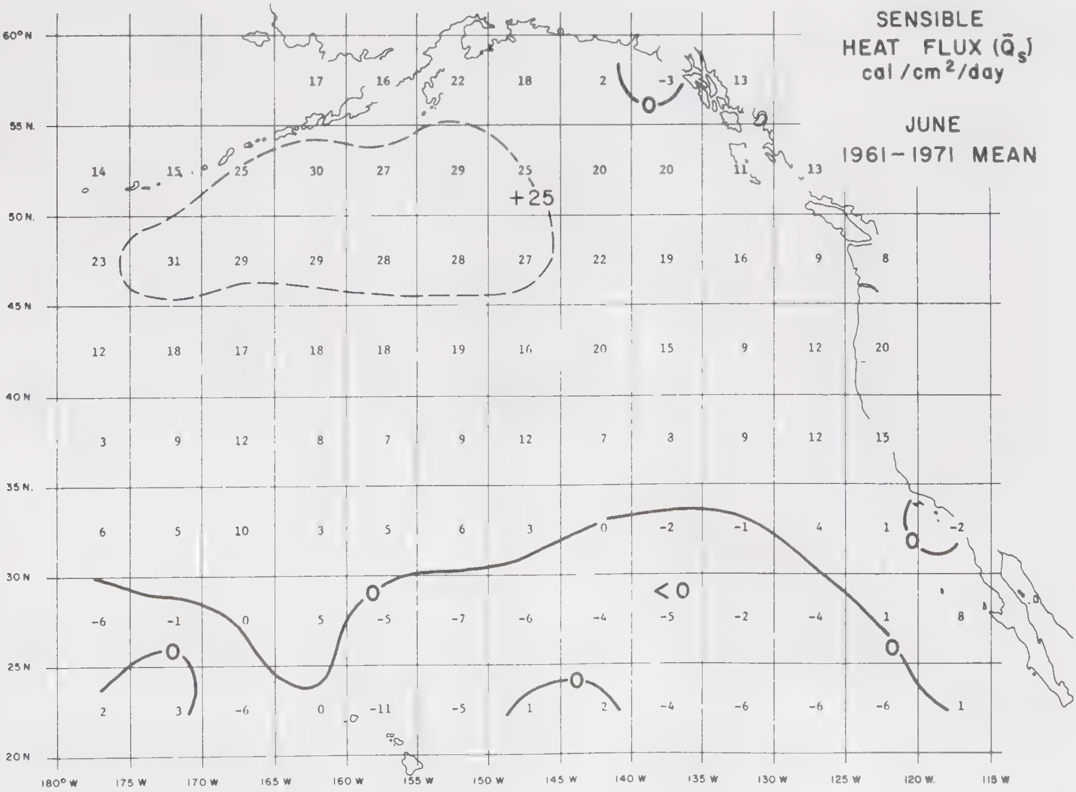

SENSIBLE HEAT FLUX ($\bar{Q}_s$)
cal / cm² / day
APRIL
1961 - 1971 MEAN
18 -3 -7 -7 -8 -22 -24
0
8 2 -1 3 2 6 7 3 -3 -14 -13
> 0
10 14 10 7 7 8 7 3 7 4 4 -8
-6 6 1 7 2 7 -4 -4 -7 -2 -5 1
0
-9 -9 -5 -5 -8 -8 -9 -10 -12 -11 -7 0 1
-8 -10 -8 -8 -4 -5 -8 -10 -14 -13 -10 -4 -2
< 0
-16 -16 -11 -12 -14 -22 -21 -17 -14 -13 -14 -7 0 7
-18 -17 -26 -14 -19 -18 -7 -7 -9 -11 -11 -12 -10
60° N. 55 N. 50 N. 45 N. 40 N. 35 N. 30 N. 25 N. 20 N.
180° W. 175 W. 170 W. 165 W. 160 W. 155 W. 150 W. 145 W. 140 W. 135 W. 130 W. 125 W. 120 W. 115 W.



SENSIBLE HEAT FLUX ($\bar{Q}_s$) cal/cm^2/day

MAY 1961–1971 MEAN

60° N.
55 N.
50 N.
45 N.
40 N.
35 N.
30 N
25 N.
20 N.
180° W.
175 W.
170 W.
165 W.
160 W.
155 W.
150 W.
145 W.
140 W
135 W.
130 W
125 W.
120 W.
115 W.
9 3 15 12 -4 -8 -6
0
6 8 11 19 21 20 22 19 17 26
24 23 20 22 23 26 20 21 18 14 8 7
>0
12 8 11 10 7 10 12 14 8 5 4 9
-4 1 -1 2 2 2 1 1 -1 1 1 5
0
-7 -5 0 -2 -2 1 -3 -4 -8 -7 -3 0 2 -2
-7 -10 -9 -6 -7 -16 -12 -10 -9 -5 -5 -6 6
<0
0
-6 -3 -10 -8 -9 -10 -10 -5 -9 -3 -7 -7 -7



SENSIBLE HEAT FLUX ($\bar{Q}_s$) cal/cm^2/day

JUNE 1961–1971 MEAN

60° N
55 N.
50 N.
45 N
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30 N
25 N
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180° W
175 W
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165 W
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150 W
145 W
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135 W
130 W
125 W
120 W.
115 W
17 16 22 18 2 -3 13
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14 15 25 30 27 29 25 20 20 11 13
+25
23 31 29 29 28 28 27 22 19 16 9 8
12 18 17 18 18 19 16 20 15 9 12 20
3 9 12 8 7 9 12 7 3 9 12 15
6 5 10 3 5 6 3 0 -2 -1 4 1 -2
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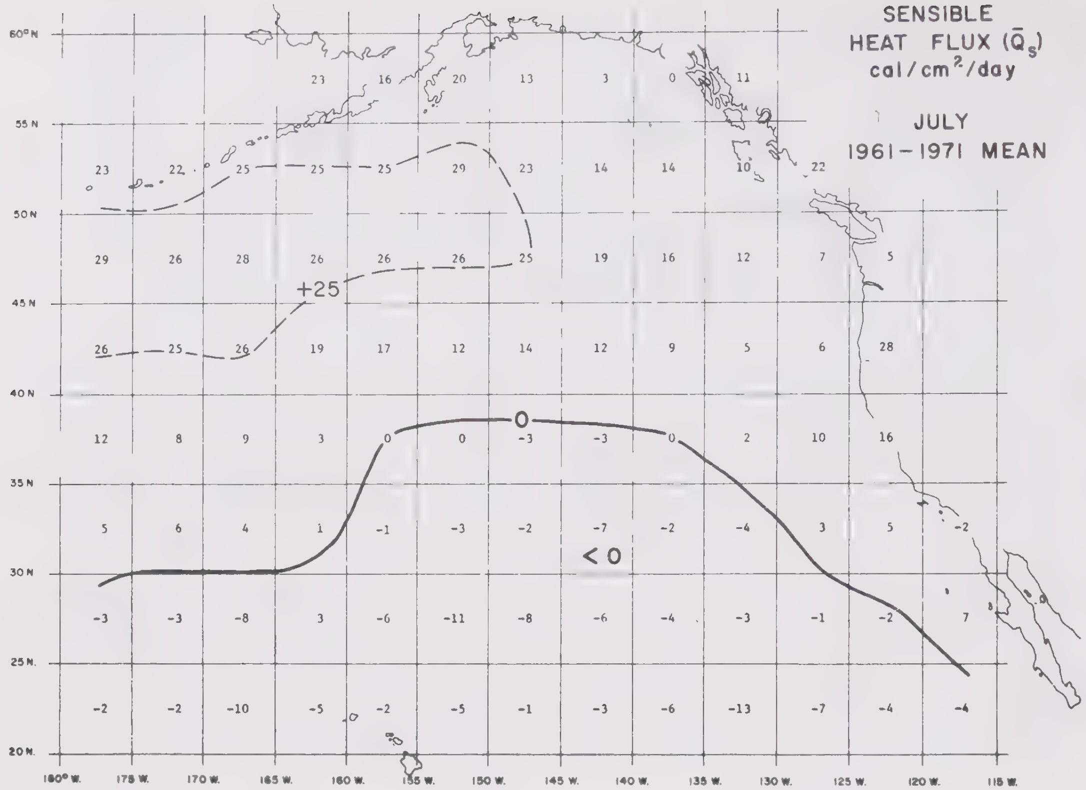

SENSIBLE HEAT FLUX ($\bar{Q}_s$) cal/cm^2/day

JULY 1961-1971 MEAN

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29 26 28 26 26 26 25 19 16 12 7 5
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26 25 26 19 17 12 14 12 9 5 6 28
0
12 8 9 3 0 0 -3 -3 0 2 10 16
5 6 4 1 -1 -3 -2 -7 -2 -4 3 5 -2
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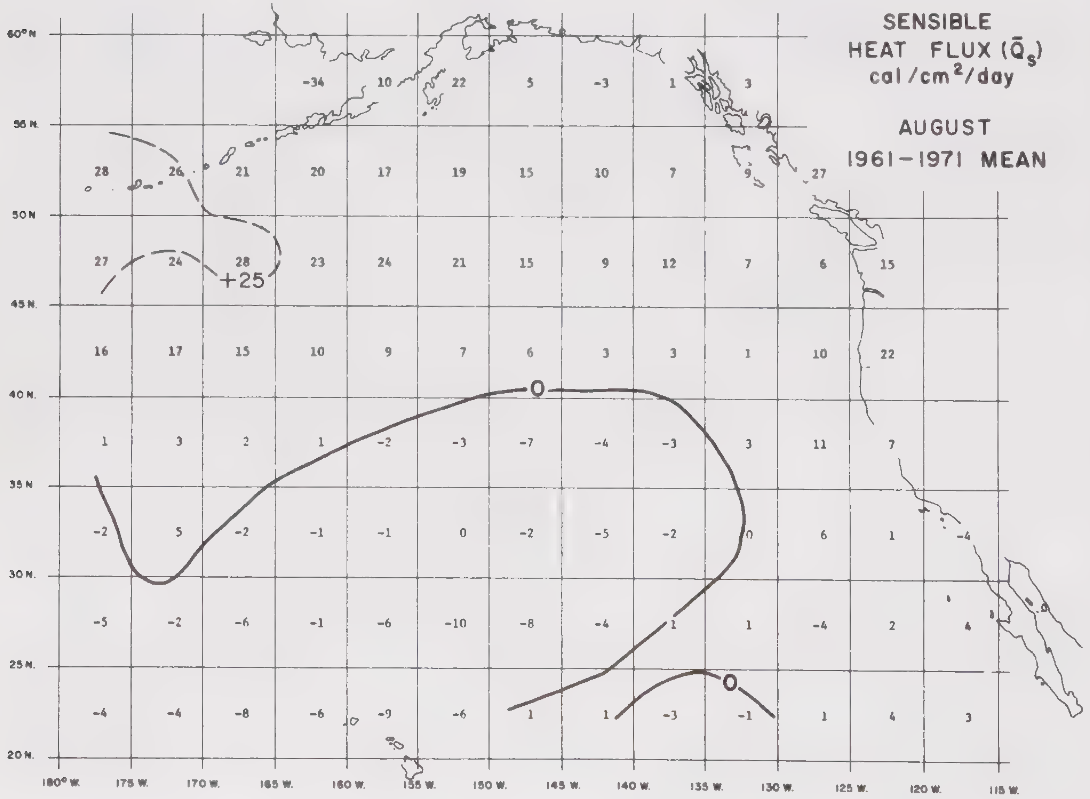

SENSIBLE HEAT FLUX ($\bar{Q}_s$) cal/cm^2/day

AUGUST 1961-1971 MEAN

60° N
55 N.
50 N.
45 N.
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35 N
30 N.
25 N.
20 N.
-34 10 22 5 -3 1 3
28 26 21 20 17 19 15 10 7 9 27
27 24 28 23 24 21 15 9 12 7 6 15
+25
16 17 15 10 9 7 6 3 3 1 10 22
0
1 3 2 1 -2 -3 -7 -4 -3 3 11 7
-2 5 -2 -1 -1 0 -2 -5 -2 0 6 1 -4
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0
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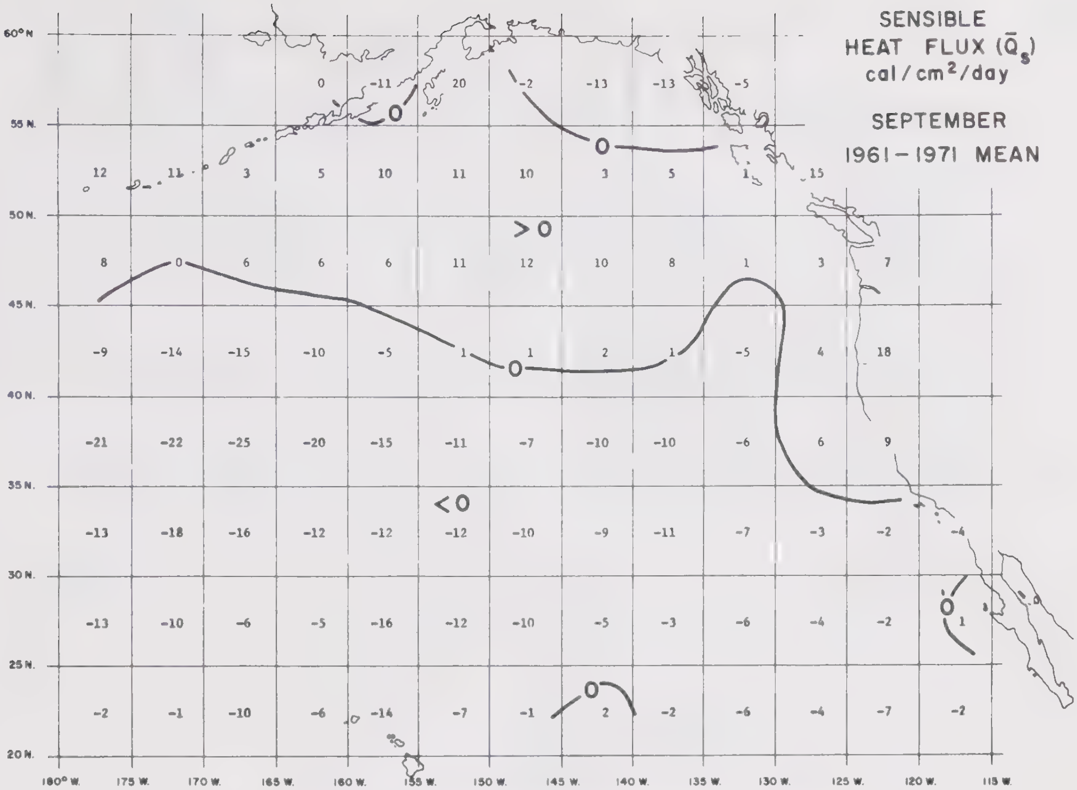
SENSIBLE
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cal/cm²/day
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20 N.
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-21 -22 -25 -20 -15 -11 -7 -10 -10 -6 6 9
-13 -18 -16 -12 -12 -12 -10 -9 -11 -7 -3 -2 -4
-13 -10 -6 -5 -16 -12 -10 -5 -3 -6 -4 -2 1
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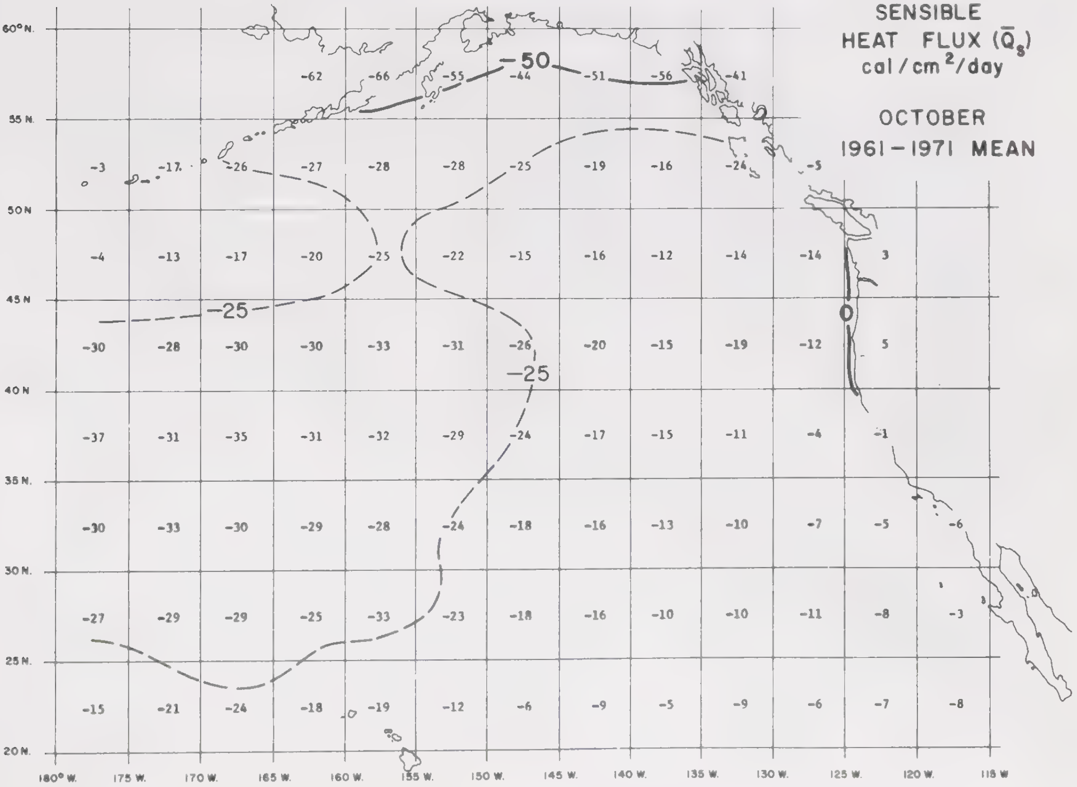
SENSIBLE
HEAT FLUX ($\bar{Q}_s$)
cal/cm²/day
OCTOBER
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60° N.
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135 W.
130 W.
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-62 -66 -55 -44 -51 -56 -41
-3 -17 -26 -27 -28 -28 -25 -19 -16 -24 -5
-4 -13 -17 -20 -25 -22 -15 -16 -12 -14 -14 3
-30 -28 -30 -30 -33 -31 -26 -20 -15 -19 -12 5
-37 -31 -35 -31 -32 -29 -24 -17 -15 -11 -4 -1
-30 -33 -30 -29 -28 -24 -18 -16 -13 -10 -7 -5 -6
-27 -29 -29 -25 -33 -23 -18 -16 -10 -10 -11 -8 -3
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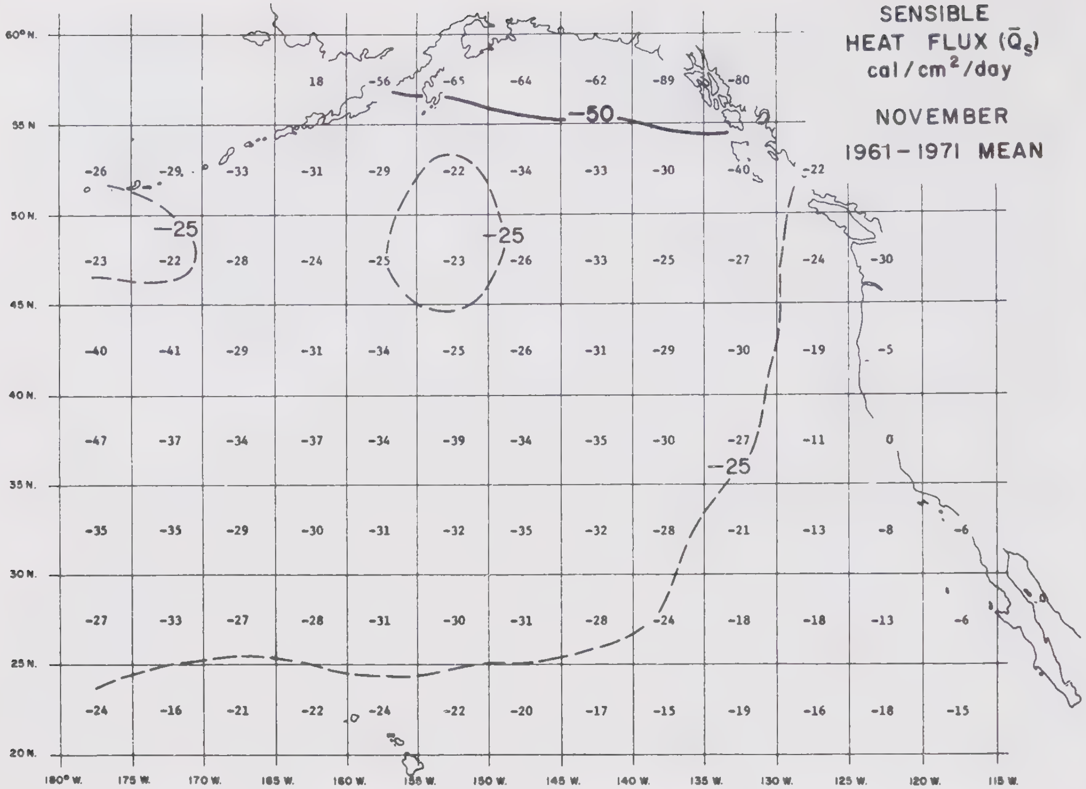
SENSIBLE
HEAT FLUX ($\bar{Q}_s$)
cal/cm²/day
NOVEMBER
1961 - 1971 MEAN
60° N.
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25 N.
20 N.
180° W.
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-35 -35 -29 -30 -31 -32 -35 -32 -28 -21 -13 -8 -6
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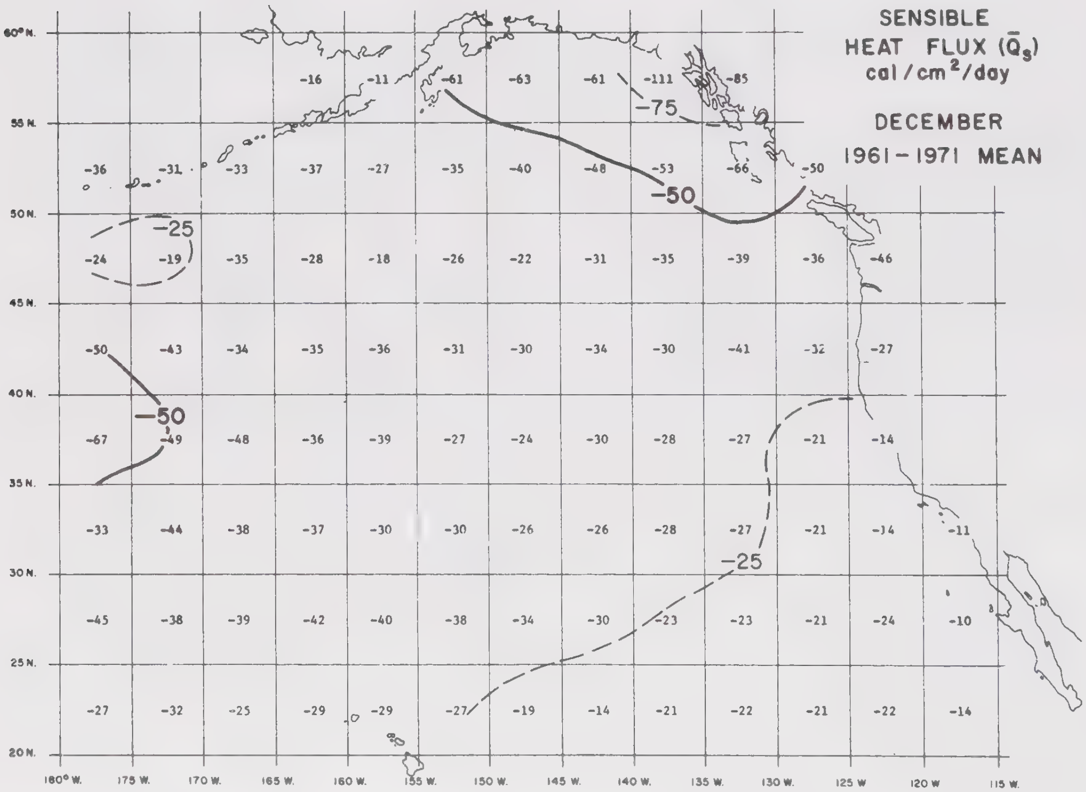
SENSIBLE
HEAT FLUX ($\bar{Q}_s$)
cal/cm²/day
DECEMBER
1961 - 1971 MEAN
60° N.
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-50 -43 -34 -35 -36 -31 -30 -34 -30 -41 -32 -27
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-67 -49 -48 -36 -39 -27 -24 -30 -28 -27 -21 -14
-33 -44 -38 -37 -30 -30 -26 -26 -28 -27 -21 -14 -11
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SENSITIVITY OF RESTRAINED SKIPJACK TUNA (*KATSUWONUS PELAMIS*) TO ABRUPT INCREASES IN TEMPERATURE[*]

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Abstract—1. Restrained skipjack tuna (*Katsuwonus pelamis*) signaled by deceleration of heart rate that they could perceive abrupt temperature increases (1°C/sec) as small as 1°C.

2. A thermal stimulus directed into the oral-branchial cavity was more effective in eliciting responses than stimuli delivered to the nasal cavity or the dorsal, anterior quadrant of the body surface. This finding is discussed in relation to the current belief that thermal sensors in fish are generously scattered over the skin surface.

INTRODUCTION

A TEMPERATURE-DETECTING mechanism that facilitates behavioral thermoregulation is adaptively important to fishes, because thermal heterogeneity is characteristic of the aquatic environment and temperature dramatically affects biological systems. The temperature sense of tunas must be especially acute if they are to perceive and make directed responses to the very gradual horizontal temperature gradients and fronts of the open ocean (0·001–0·1°C/100 m). That tunas do made directed responses to these gradients of temperature can be inferred from the close correspondence between certain sea-surface isotherms and the limits of tuna distribution (Blackburn, 1965).

Although the sensitivity of nonpelagic marine fish to environmental temperature change has been well documented (0·03–0·10°C, summarized by Murray, 1971), only casual and indirect observations have been made on temperature perception in tunas. Gooding & Higgins noted that skipjack tuna (*Katsuwonus pelamis*) stayed above a 15°C discontinuity layer in a vertical temperature gradient

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(R. M. Gooding & B. E. Higgins, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, personal communication). Laurs *et al.* (1970) reported that a sonic-tagged albacore (*Thunnus alalunga*) seemed to avoid a thermal front of 0·1°C/100 m. Green (1967) found that purse seining for tuna was most effective when a temperature discontinuity layer (thermocline) of at least 0·5°C/m deterred escape through the bottom opening of the seine. In these cases temperature seems to be the main orienting cue, but no systematic attempts have been made to eliminate other concomitant cues such as pressure, light, turbidity, oxygen and olfactory quality of the water.

In this paper, we (1) test whether restrained skipjack tuna will respond to abrupt temperature changes, (2) compare sensitivity of the oral-branchial cavity, the olfactory cavity and the skin and (3) provide a first estimate of temperature threshold for a pelagic oceanic fish. Classical heart-rate conditioning was the method used. This technique has been successfully used on fish—most recently by Rommel & McCleave (1972) to determine perception of electric fields by eels. We are the first to use this technique to evaluate temperature perception. Application of the test for our purposes required demonstration that the observed responses (abrupt heart rate decelerations) were time-related to the temperature stimulus. The chief advantage of the method is speed of application—2 hr is sufficient to demonstrate temperature-related responses. The fragility of skipjack tuna in captivity obviates any long-term experimentation or methods that require extensive handling.

MATERIALS AND METHODS

Forty-one skipjack tuna (average weight 1·5 kg) were tested. Stocks were held at the Kewalo Basin Tuna Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, Hawaii. Techniques of maintaining tuna in captivity have been outlined by Nakamura (1972).

Experimental sessions were conducted at night, when the fish were easier to capture and tolerated restraint better. Two fish were tested each night in sessions that lasted approximately 2 hr per fish. For training, we secured the fish in a trough constructed from polyvinyl chloride pipe and padded with plastic foam. Velcro* strapping and an injection of a muscle relaxant (gallamine triethiodide, 1 mg/kg) were necessary to keep the fish sufficiently immobile so that muscle potentials did not interfere with the electrocardiogram (EKG) recording. Water for respiration was delivered at 8 l./min via a rubber tube secured in the fish's mouth. We kept a skipjack tuna alive for 8 hr under these conditions and had no mortalities during the usual 2-hr training sessions. During testing, the fish were isolated; all recording and stimulus preparation was done from an adjacent room to eliminate disturbances to the fish.

Temperature of the stimulus water and the heartbeat were continuously monitored.

We recorded temperature with a fast-responding copper-constantin thermocouple (Omega Engineering, Model SPSS-020U-6). The temperature signal was amplified in the upper channel vertical amplifier of a dual-channel oscilloscope (Textronix, Model 5030) and recorded (Brush, Model 220, two-channel paper recorder).

The EKG was recorded via fine wires inserted under the skin and adjacent to the heart. The signal was amplified and filtered (100–1000 Hz) to improve signal-to-noise characteristics (PAR Instruments, Model 113) and displayed visually on the lower channel

* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

of the oscilloscope. The oscilloscope sweep was triggered by each heartbeat. The "gate output" of the oscilloscope was used to reset the analog integral of the output of a free-running multivibrator. These two circuits (multivibrator and integrator) were "patched" on an analog operational manifold (Teledyne Philbrick Instruments). The resultant sawtooth output, along with the stimulus temperature, was recorded with the paper recorder. Each sawtooth represented one heartbeat and the height of each "tooth" was directly proportional to the interbeat interval.

We used two different types of unconditioned stimuli (US): (1) water perfusing the gills momentarily shut off or (2) an electric shock. The unconditioned response (UR) in each case was an immediate cessation in the heartbeat followed by several irregularly spaced beats. For each fish one of three conditioned stimuli (CS) was applied: temperature stimuli directed to (1) the oral-branchial cavity (mouth), (2) the right nasal capsule (nose) or (3) the dorsal, anterior quadrant of the body (back). For the mouth stimulus, the temperature of the water flow through the oral-branchial cavity to the gills was altered. Water flows and maximum temperature rises under the three stimulus conditions were 100 ml/min up to +10°C for the nose and 8 l./min at +6°C for both mouth and back. Ambient temperature of the perfusion water was between 24 and 25°C. Stimulus flows were continuous; temperature was altered by heating a stainless steel segment inserted into the supply line. Application of heat ended approximately 30 sec before the temperature change reached the fish and thus reduced the possibility that the fish received other cues associated with changing the water temperature.

The US was applied when the temperature reached +6°C, except for two mouth-stimulated fish (B and F) in which the US was delivered at +5°C. This resulted in a 10-sec delay between the initial temperature rise and the US. Fish were trained for thirty trials; intertrial intervals were 2–4 min.

RESULTS

Of the forty-one fish examined, eight were tested with temperature stimuli delivered to the mouth; six of these were responsive. Ten fish were tested with stimuli delivered to the back; three were responsive. Twenty-three fish were tested with stimuli delivered to the nose; eight were responsive. Over 50 per cent of the fish tested were considered unresponsive. In most of these cases, no heartbeat decelerations were observed during temperature change; in others, the heart rate was so irregular it was impossible to discern responses.

Figure 1 illustrates typical heart-rate responses. In Fig. 1a the temperature stimulus was delivered to the nose and a response (decrease in heart rate) occurred at about 5°C. After the temperature reached 6°C, the US was applied and the UR (another decrease in heart rate) followed. In Fig. 1b the stimulus was delivered to the mouth and a decrease appeared almost simultaneously with the initial temperature rise. In this example spontaneous responses occurred before and after the trial. The question arises whether the simultaneous decrease was in response to the temperature stimulus or spontaneous. Because abrupt spontaneous decreases in heart rate were characteristic of most fish tested, a careful statistical evaluation of the data was necessitated to determine whether observed responses were in fact controlled by the thermal stimulus.

To distinguish spontaneous responses from responses to temperature, the frequencies of responses in the intertrial period were compared to the frequencies of responses during the period when the temperature was rising prior to the US

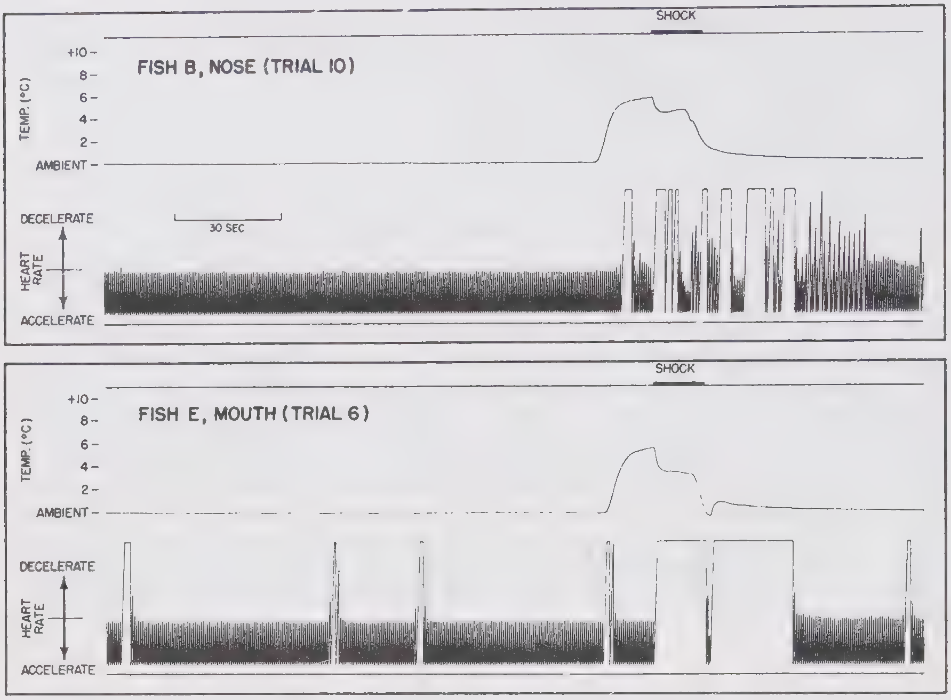

Fig. 1a. A recording from a skipjack tuna showing deceleration in heart rate, accompanying a temperature rise in the naris and then an electric shock (trial 10, fish B, nose). b. A similar record except that the temperature change occurred in the mouth and spontaneous decelerations occurred before and after the trial period (trial 6, fish E, mouth).

(Kolmogorov–Smirnov one-sample test; Siegel, 1956). Two of the six responsive fish stimulated in the mouth and one of the eight responsive fish stimulated in the nose had significantly greater frequencies of response during the temperature stimulus period than during the intertrial period ($P \leqslant 0{\cdot}05$; Table 1). Combining the data for the six analyzed fish stimulated in the mouth indicated that the frequencies of response were significantly greater during the stimulus period ($P \leqslant 0{\cdot}05$). The similarly combined data for the eight analyzed fish stimulated in the nose were also statistically significant ($P \leqslant 0{\cdot}05$). Combined data for all seventeen analyzed fish (in Table 1) yielded a highly significant difference in frequencies of response between the intertrial period and the period during the temperature change ($P \leqslant 0{\cdot}01$). We conclude that restrained skipjack tuna responded to water temperature change with a decreased heart rate.

To obtain an estimate of threshold of response, the temperature stimuli were grouped by 1°C intervals. Frequencies of response were then plotted for individual fish as a function of stimulus temperature (Fig. 2).

TABLE 1—TIME (sec), NUMBER OF RESPONSES AND RESPONSE FREQUENCIES OF SKIPJACK TUNA BEFORE TEMPERATURE STIMULATION (INTERTRIAL) AND DURING STIMULATION (TRIAL)

		Intertrial (No temperature change)			Trial (During temperature change)			
Stimulus position	Fish	Time (sec)	No. of responses	Responses per sec	Time (sec)	No. of responses	Responses per sec	Level of significance
Mouth	A	4476	86	0·019	717	42	0·059	Significant at 0·01
	B	4581	100	0·022	414	26	0·063	Significant at 0·05
	C	4803	65	0·014	295	4	0·014	—
	D	5040	134	0·027	380	26	0·068	—
	E	3052	121	0·040	237	19	0·080	—
	F	4258	81	0·019	510	19	0·037	—
Total		26,210	587	0·022	2553	136	0·053	Significant at 0·05
Nose	A	3074	109	0·035	589	42	0·071	Significant at 0·05
	B	6414	45	0·007	1508	19	0·013	—
	C	2081	58	0·028	594	15	0·025	—
	D	3055	42	0·014	446	11	0·025	—
	E	3942	100	0·025	732	19	0·026	—
	F	2919	35	0·012	1224	16	0·013	—
	G	4839	65	0·013	566	13	0·023	—
	M	3303	53	0·016	347	12	0·035	—
Total		29,627	507	0·017	6006	147	0·024	Significant at 0·05
Back	A	4866	138	0·028	361	9	0·025	—
	B	7137	172	0·024	517	21	0·041	—
	C	4545	88	0·019	347	18	0·052	—
Total		16,548	398	0·024	1225	48	0·039	—
Grand total		72,385	1492	0·021	9784	331	0·034	Significant at 0·01

Level of significance of differences in distribution of observed values (responses) and distribution of "effort" (time) was determined by the Kolmogorov–Smirnov one-sample test (Siegel, 1956).

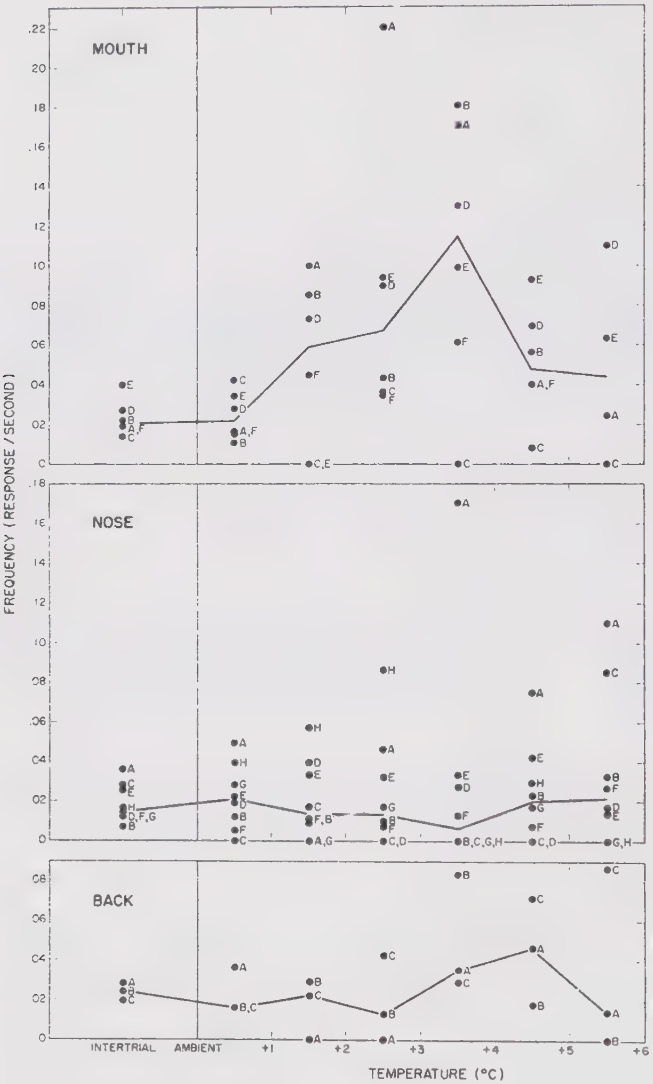

Fig. 2a. Response (heart beat rate decelerations) frequencies of six skipjack tuna before temperature stimulation (intertrial period) and during temperature stimulation by 1°C intervals. The temperature stimulus was applied to the mouth. b. Response frequencies of nine skipjack tuna to temperature stimuli in the nose. c. Response frequencies of three skipjack tuna to temperature stimuli on the back.

Temperature stimuli delivered to the mouth produced the most dramatic results (Fig. 2a). Frequencies of response varied significantly with temperature (Friedman two-way AOV by ranks, $0{\cdot}01 < P < 0{\cdot}02$; Siegel, 1956). Median response frequency of the six fish was maximal in the +3 to +4°C interval, but an increase in the median was apparent in the +1 to +2°C interval.

The median frequency of response of the nose-stimulated fish did not vary significantly with temperature (Fig. 2b, Friedman test). Yet the one fish with a significant temperature effect (fish A) had the greatest frequency of response in the +3 to +4°C interval—similar to the mouth-stimulated fish.

Three responsive fish tested with stimuli directed to the back provided too little data to test statistically. However, there was a hint of increased responsiveness in the +3 to +5°C interval (Fig. 2c).

DISCUSSION

Temperature sensitivity

Work by Bull (1936), interpreted by Harden Jones (1968), demonstrated that a large variety of marine fishes in an unrestrained training situation and with prolonged conditioning can perceive temperature changes of about +0·03°C when the change occurs within 1–10 sec. In contrast, skipjack tuna stimulated in the mouth demonstrated perception in the +1 to +2°C temperature band (Fig. 2a). This change occurred within 1–2 sec. Under our experimental conditions skipjack tuna seemed to be less sensitive to rapid temperature changes than other fishes, by about two orders of magnitude. If this first estimate of temperature sensitivity is realistic, skipjack tuna would be able to perceive a relatively abrupt thermocline (0·5°C/m) but not the very gradual horizontal gradients (0·001–0·1°C/100 m) of the open sea unless they possess a mechanism for long-term thermal "memory". Then, successive comparisons could be made that are sufficiently spaced in time in order for the necessary temperature difference of approximately 1°C to accrue. This would take about 20 min for a 0·50-m skipjack tuna swimming in a 0·1°C/100 m gradient at about two body lengths per sec.

By the methods employed skipjack tuna can perceive a temperature change of *at least* +1°C if the change occurs in 1 sec. Free-swimming unstressed fish can, no doubt, do better. Several factors contributed to reduce the performance of our fish:

(1) No fish died during the 2-hr testing period and heart rates were (for the most part) constant; nevertheless, it was obvious that restraint is a highly artificial situation for tuna involving a barrage of unfamiliar, confusing and conflicting stimuli. These extraneous stimuli serve to mask and divert attention from the temperature change. Heart rates were generally higher (100–150 beats/min) than those observed in free-swimming tuna (75–125 beats/min), which suggests an excited state. Yet, previous experiments with hardier tilapia (*Tilapia mossambica*) using similar techniques yielded similar thresholds.

(2) Because the temperature rise (CS) was gradual and not a step function, latency of response is confounded with sensory thresholds. It is conceivable that perception occurred at a smaller ΔT but the delay in organizing responses produced the apparent 1°C thresholds. However, the fish demonstrated almost no

delay in responding to the US. Furthermore, there was no consistency in latencies of response when different temperature slopes were employed. A slower rate of temperature change did not result in lower thresholds.

(3) Although actual conditioning of the fish to the temperature stimuli was desired, our results were not dependent upon it. It was sufficient to demonstrate that the observed responses were in some way controlled by the temperature stimulus. The tuna probably responded because the stimuli were of sufficiently high intensity. The fish did not have to learn an association between the noxious US and a weak CS. For this reason, responses were observed in many cases (especially with mouth stimuli) on the first trial. Perhaps repeated pairings of very weak temperature stimuli and the US would have eventually yielded lower thresholds. Bull (1936) had to train his free-swimming subjects for 2 months to obtain 0·03°C values. He found that as training progressed fish would respond with shorter latency after the onset of the temperature change. Rommel & McCleave (1972) required at least eighty trials to determine electric field thresholds. Yet, we observed no improvement in performance (response occurring at progressively lower temperature) when responding fish were trained for over thirty trials. Furthermore, if responses were not present after about fifteen trials, they did not appear after more trials. We strongly suspect that the declining condition of our restrained tuna made successful conditioning increasingly more difficult as the experimental session progressed.

Location of sensors

Thermal stimuli delivered to the oral-branchial cavity of skipjack tuna produced relatively the best responses. But, current belief holds that free-nerve endings in the skin over the entire body surface serve as the temperature sensors in fishes (Murray, 1971). This contention is based on little evidence. Response latencies from free-swimming fish preclude mediation by anything but surface receptors (Bull, 1936; Dijkgraaf, 1940). The unpublished cocaine treatment studies of Sullivan & Fisher (Sullivan, 1954) are most frequently cited as the definitive evidence of scattered, cutaneous thermal sensitivity; trout, whose body surfaces were desensitized by cocaine, failed to select temperature in a gradient.

Yet when temperature stimuli have been directed exclusively to the skin surface (summarized by Murray, 1971), response thresholds were higher by at least two orders of magnitude than those of free-swimming fish. Our results corroborate a lack of sensitivity in the skin surface. Free-swimming fishes have low temperature thresholds; our tuna seemed most sensitive to thermal stimuli directed into the mouth. In both situations, receptors in the oral-branchial cavity are exposed to temperature changes.

Alternatively, temperature perception (mouth vs. skin) in skipjack tuna may be different from that in other fishes. Free nerve endings in the skin of skipjack tuna are not found distal to a 150-μ deep layer of chromatophores. Other teleosts have endings virtually at the skin surface (J. I. Kendall, Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, personal communication).

Perhaps denervation of the outermost skin surface has occurred concurrently with other adaptations of the skin of the tuna for continuous, fast swimming. Tactile sense may have been lost or downgraded in importance. Certainly the importance of a tactile sense should be less in a pelagic fish than in fish living near solid objects. In tuna, contact with any object except prey is very unusual; if it happens, damage to the tissues usually occurs. Another sensory restriction commensurate with a pelagic lifestyle does exist in tunas. In contrast to all other teleosts so far examined, skipjack tuna lack color vision (Tamura *et al.*, 1972). Skipjack tuna live in a virtually monochromatic environment.

From the data presented, we conclude that skipjack tuna do perceive abrupt temperature changes of at least +1°C with the greatest sensitivity within the oral-branchial cavity. This provides a first estimate of temperature threshold for a pelagic oceanic fish and is the first time cardiac conditioning has been used to evaluate thermal responses. Ongoing work is examining thresholds in free-swimming tuna and thresholds of temperature decreases of restrained tuna.

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Key Word Index—Temperature perception; tunas; thermoregulation; classical conditioning

7408

Some Biological Observations of Billfishes Taken in the Eastern Pacific Ocean, 1967-1970

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ABSTRACT

From 1967 through 1970 sport-caught billfishes were sampled at Mazatlán, Sinaloa; and Buena Vista, Baja California, and at San Diego, California. Lengths, weights, morphometrics, meristics, and gonad data were gathered on a total of 2,056 striped marlin, 821 sailfish, 61 blue marlin, and 1 black marlin. This paper presents information on reproduction, average length and condition factor, food habits for 1970, and notes on parasites.

Developing gonads were found only in the Mexican fish. Our data on reproduction indicated that both striped marlin and sailfish spawn once per year with peak spawning activity probably in June and July. There is also the possibility that sailfish spawn in other months. First maturity in striped marlin and sailfish occurred in the 155-165 cm eye-fork length class. Fecundity estimates ranged from 2 to 5 million eggs for four sailfish and from 11 to 29 million eggs for three striped marlin. It appears tnat striped marlin move offshore from the Mexican coastline to spawn while sailfish remain closer to shore.

Much of the interest in billfishes in the eastern acific Ocean stems from their popularity among oort fishermen. Commercial fishermen have also een interested in the billfish resources as indicated their extensive and continuous operation in this ea since 1956 (Suda and Schaefer, 1965). Since 963 this fishery has concentrated off Mexico where is directed primarily at striped marlin *(Tetrapturus udax)* and sailfish *(Istiophorus platypterus)* (Kume id Schaefer, 1966; Kume and Joseph, 1969a). hroughout the history of the billfish fishery in the astern Pacific no attempt has been made to manage ese resources; this is partly due to the lack of formation on the life history and population ynamics of these fishes. This report provides data athered from billfishes landed at sportfishing sites southern California and Mexico from 1967 to 970. Specimens were examined at San Diego, alifornia; Buena Vista, Baja California; and lazatlán, Sinaloa, Mexico (Fig. 1). A total of 2,056 riped marlin, 821 sailfish, 61 blue marlin (*Makaira gricans*) and 1 black marlin (*M. indica*) ere sampled. This paper is one of a series of publications describing the results of these studies. Evans and Wares (1972) published information of the food habits of fish collected in 1967-1969, and another paper (Wares and Sakagawa, 1973) has been prepared to present meristic and morphometric analyses.

The purpose of this paper is primarily to present

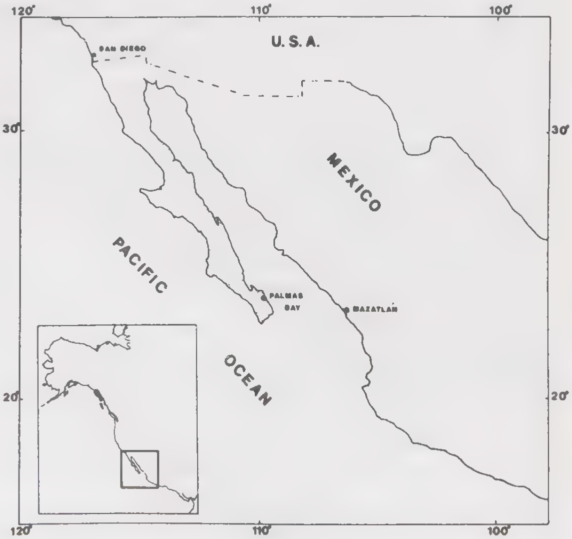

Figure 1.—Location of the three billfish sampling sites.

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data relating to sexual maturation and to make inferences on the reproductive biology of striped marlin and sailfish. The numbers of blue and black marlin were insufficient to add significantly to the knowledge of these species. We also present notes on food habits as observed from data collected in 1970, seasonal abundance, and parasites.

Because of the long established fishery for billfishes in the western and central Pacific, most billfish reproduction information has been derived from that area (Nakamura, 1932, 1940, 1949; Ueyanagi, 1959; Yabe, 1953; Honma and Kamimura, 1958). Merrett (1970, 1971) and Williams (1963, 1964, and 1970) reported on the Indian Ocean billfishes and concluded they are closely related to those in the western Pacific. We have encountered only two major publications (Kume and Joseph, 1969b; Yurov and Gonzales, 1972) dealing with reproduction of billfishes east of long. 130°W.

SEASONALITY

All four of the species studied occur regularly at Mazatlán and Buena Vista where they exhibit seasonal cycles of abundance. San Diego is near the northern extreme of istiophorid ranges on the eastern Pacific coast and except possibly in the warmest years, striped marlin is the only species captured there. The occurrence of striped marlin is highly seasonal.

Based on records kept by several resorts (1963-69) in the Palmas Bay area of Baja California (the area surrounding Buena Vista) and at Mazatlán (1967-69), sailfish and striped marlin show distinct patterns of seasonal abundance. Though these data are probably not highly accurate, the trends (Fig. 2 and 3) agree with our personal observations and with data provided by the Departamento de Tourismo, Terr. Baja California Sur. Seasonalities for blue and black marlin are not presented because of the low numbers in the catch records and because of persistent confusion in the identification of the two species. It appeared, however, that blue marlin were most abundant from late summer through winter, at least in the Palmas Bay area.

Peak abundance of both striped marlin and sailfish tended to occur later in the year at Palmas Bay than Mazatlán. At each location, the time of maximum abundance of sailfish occurred later than that of striped marlin. The seasonal occurrence of striped marlin is much more restricted at San Diego than in Mexico with no fish being caught before July 1 or after December 1. Records of striped marlin landed at three sportfishing clubs in San Diego from 1963 to 1970 show the peak catch to vary between late August and early October. The timing of the apparent abundance of striped marlin off San Diego is believed to be correlated with surface water temperatures (Squire, 1974a).

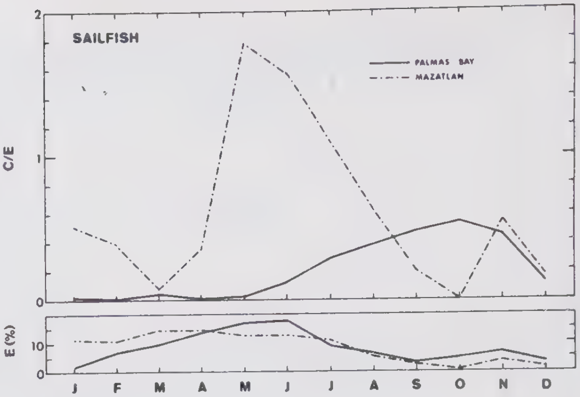

Figure 2.—Catch per unit effort (number per boat-day) and percent effort for sailfish sport fishery from Palmas Bay (1963-1969) and Mazatlán (1967-1969).

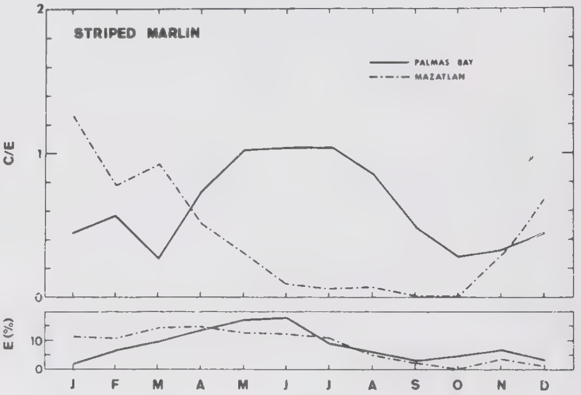

Figure 3.—Catch per unit effort (number per boat-day) and percent effort for striped marlin sport fishery from Palmas Bay (1963-1969) and Mazatlán (1967-1969).

REPRODUCTION

Collection and Processing of Samples

Gonad weights and fish length and weight were measured and sex noted of each fish examined. During 1969 and 1970 core samples of ovaries were also taken. Also in 1970, Japanese longliners provided us with gonads and detailed information of six additional mature striped marlin caught near the Revillagigedo Islands (lat. 19°N, long. 111°W).

Field sampling of specimens involved examination of fishes during the same day in which they were caught. Each fish was weighed and measured (eye-fork length). The body cavity was then opened and the gonads excised. Adhering fascia were removed and the gonads weighed. In 1970 the length and volume of each gonad was measured. During 1969 and 1970 ovarian tissue was sampled with a cork borer following a method used by Yuen (1955) wherein two transverse borings through the ovary are made at approximately ⅓ the distance from each end. These two samples from each fish were preserved in Gilson's fluid (Simpson, 1951), which rendered the ova much easier to measure and handle. This treatment appears to have no obvious differential effect on the ova diameters or shape (Schaefer and Orange, 1956).

The samples were kept in Gilson's fluid from 2 to 18 mo during which time the ova became separated from the ovarian tissue. Each sample was then gently stirred and a random sample of ova was measured with an ocular micrometer at 30× magnification. Ova diameter measurements were taken on whatever axis fell parallel to the micrometer graduations. Several authors (Clark, 1925, 1934; June, 1953; Otsu and Uchida, 1959; and Yuen, 1955) have concluded that random measurements regardless of the axis produced reliable results.

Because differential maturation of ova was found in bigeye tuna (Yuen, 1955) we took integrated samples with the cork borer. Later examination of mature striped marlin and sailfish ovaries, however, showed no evidence of either cross-sectional or longitudinal variation in ova size within ovaries. We tested for cross-sectional variation by taking radial subsamples from a 10 mm thick transverse section near the middle of one of the largest, most mature striped marlin ovaries. The ova diameter frequency distributions (Fig. 4) of three samples radiating from the center were similar. Likewise, anterior, middle, and posterior subsamples from two striped marlin and one sailfish ovaries showed no evidence of longitudinal variation (Fig. 5).

The 95th centile egg diameter was determined from the size frequency distribution of 300 eggs measured at random as described by Schaefer and Orange (1956). "Maximum ova diameter" as used by us was the largest size class interval (0.066 mm increments) containing ova from a sample of 50 ova measured at random.

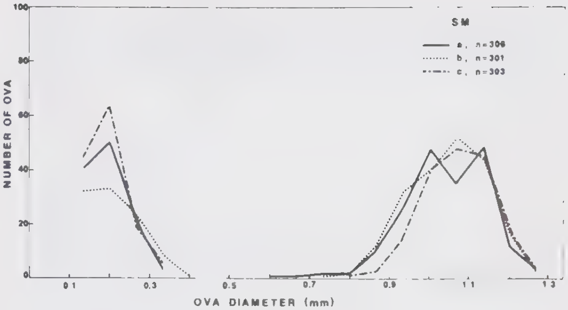

Figure 4.—Ova diameter frequency polygons of subsamples taken near the middle of a mature striped marlin ovary; **a**—central, **b**—intermediate, **c**—peripheral.

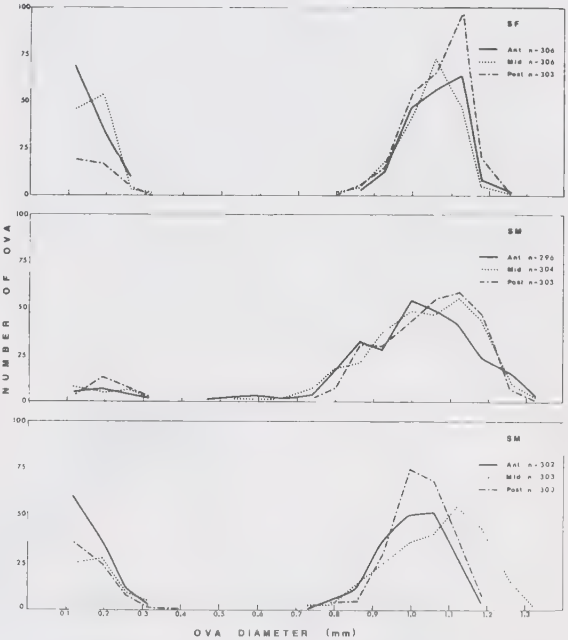

Figure 5.—Ova diameter frequency polygons from one mature sailfish and two striped marlin. Samples were taken from the anterior, middle, and posterior areas of the left ovary.

Description of Gonads

Detailed description of the gonads and spawning products of billfishes were published by Merrett (1970) and La Monte (1958). In our studies we found strong evidence of gonadal assymetry (Table 1). For striped marlin, the left gonad averaged larger than

Table 1.—Percent frequency of specimens in which the left gonad was larger in weight than the right; left gonad expressed as average percentage of combined gonad weight and length.

	Freq. L>R	Left gonad as percent of combined		
	(%)	Weight	Length	*N*
Striped Marlin				
Male	80	53.1	53.7	40
Female	95	60.5	54.5	44
Sailfish				
Male	73	48.5	53.3	11
Female	79	55.5	52.9	24

the right in both sexes. The left ovary of sailfish also averaged larger but the left testis averaged smaller in weight. Females exhibited the greatest gonadal asymmetry and the difference in size between right and left ovaries was often obvious without measurement. Williams (1963) observed similar differences in Indian Ocean striped marlin with the left gonad always larger in both length and displacement volume.

Several noteworthy gonadal abnormalities were also seen. In ten striped marlin, five sailfish, and one blue marlin, one ovary was lacking; in two striped marlin and one sailfish one testis was lacking. This phenomenon can result from the fusion of the two gonad primordia during development, or simply from the failure of one gonad to develop (Hoar and Randall, 1969). In one striped marlin the ovary had proliferated into many different sized lobes filling much of the coelomic cavity (Fig. 6). It was filled with large eggs which were visibly misshapen. Another striped marlin was noted to have a testis which had divided into separate anterior and posterior lobes. Four ovaries were tumorous, brown-red in color, consisting of dense, odiferous tissue. Penellid copepods were found encysted in the gonads of three striped marlin and one sailfish.

Measures of Sexual Maturity

The general problem of finding an accurate and efficient means of measuring sexual maturity in fishes has resulted in the development of many techniques. Testes have not been found to be suitable because of problems encountered in measuring accurately their sex products (June, 1953). In addition, Merrett (1970) has shown by histological examination that unlike the case in most teleosts, there is differential maturation of spermatozoa in the testicular lobules of billfishes. There is thus only a small

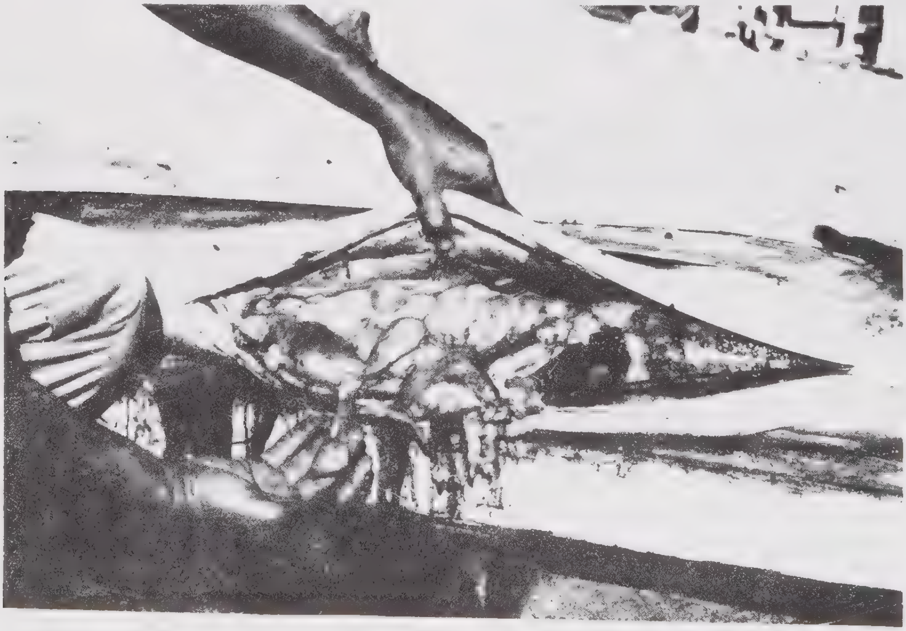

Figure 6.—Illustration of an abnormal striped marlin ovary with different sized lobes throughout the coelomic cavity.

overall seasonal increase in size of the testes, and some milt is usually present throughout the year.

On the other hand, the ovary as an indicator of maturity has been well documented (Clark, 1925, 1929, 1934; Hickling and Rutenberg, 1936). As oogenesis proceeds, characteristic changes occur which can be easily detected macroscopically or microscopically. We therefore chose to use ovarian characteristics to represent maturity of billfishes in this study.

The most precise method of determining the stage of ovarian maturity is to histologically examine the tissues as performed by Merrett (1970) or Moser (1967). This procedure, however, is lengthy and time-consuming. Another reliable technique is to measure a large number of ova from the same ovary, a method used for many species (Clark, 1929, 1934; June, 1953; and Brock, 1954). This method is based on the assumption that as the spawning season progresses, the group or groups of maturing ova will be distinguished as advancing modes in size-frequency distributions. This method is also time-consuming and laborious, but has a definite advantage in characterizing the frequency of spawning when a fully mature specimen is examined. When many fish are examined over a time interval, the progression of the modes of developing ova may provide information on the rate of maturation, time of spawning, and size at maturity. Two variations of this process which require the measurement of fewer ova are the use of "maximum ova diameter" (Otsu and Uchida, 1959) and the position of the 95th centile (Schaefer and Orange, 1956). The latter is particularly useful when the exact position of the developing mode is difficult to distinguish, as in early maturation stages.

Indirect methods to measure sexual maturity involve the relationship between some measure of the fish's size (either length or weight) and gonad weight. The use of fish length assumes that fish weight is nearly proportional to the cube of the length, a true situation with regard to the billfishes in this study as determined by length-weight analyses for eastern Pacific billfish. It is also assumed that fecundity is proportional to size. Kume and Joseph (1969b) have plotted ovary weight versus eye-fork length and also utilized the gonad index *(GI)* computed as

$$GI = (W/L^3) \cdot 10^4$$

where

W = total weight of gonads in grams, and
L = eye-fork length in cm.

Table 2.—Regression of maximum ova diameter and 95th centile of ova diameter on gonad index (n = sample size, r = coefficient of correlation, b = slope, a = y axis intercept.)

	n	r	b	a
Striped Marlin				
95th centile on GI	31	0.936*	3.02	1.46
Max. ova diameter on GI	269	0.797*	3.78	1.48
Sailfish				
95th centile on GI	21	0.913*	3.91	2.47
Max. ova diameter on GI	184	0.859*	4.78	3.43

*Significant at 0.01 level.

Merrett (1971) used another type of gonad maturation index which related the macroscopic appearance (color, yolk presence, egg diameter, and general appearance) of the gonad to recognizable stages in its histology.

To evaluate these different measures of maturity and to determine the degree of correlation between them, we applied regression analyses to our data (Table 2). As can be seen, the gonad index is highly correlated. In each of the four regressions, the correlation coefficients exceeded the 0.01 significance levels when tested against a Student's t-distribution. The lower r values for regression of maximum ova diameter on gonad index can be explained by the fact that maximum egg diameters do not always represent the size of the advanced mode. For example, the presence of a few residual eggs in an ovary which is in the resting or early maturation stages will not reflect the true stage of development of the ovary.

We have included both direct and indirect methods to analyze the spawning of striped marlin and sailfish. But, based on the above comparison and considering the time and manpower costs and the degree of accuracy desired, we conclude that the gonad index represents the most practical indicator of the stage of sexual maturity for a study of this type.

Size at First Spawning

The reported size at which striped marlin attain sexual maturity varies little among previous studies. Merrett (1971) reported first maturity at 140-160 cm eye-fork length. This agrees with the conclusion of Williams (1963). Kume and Joseph (1969b) stated that individuals greater than 160 cm from the eastern Pacific regularly occur in the spawning group (3.0 *GI*), however, they did collect a mature specimen in the 148-cm class.

Our criteria for evidence of sexual maturity were based on a minimum egg diameter and a minimum gonad index. Fish with maximum ova diameters equal to or greater than 0.3 mm were considered mature based on the work of Merrett (1970) who considered eggs of this size as maturing, having completed yolk and chorion formation. We somewhat conservatively chose $GI = 1.0$ as the other criterion based on our data (Fig. 7 and 8) which show that no gonad index exceeded 1.0 in Quarter I and, further, the gonad indices for immature fish below 145-150 cm in Quarter II were remarkably consistent and did not exceed 0.3. The increase in average gonad index with increasing fish lengths between 150 and 190 cm in Quarter II suggests that larger fish either mature earlier or have larger gonad index values at given maturity stages than smaller fish. The presence of higher gonad indices for large fish in Quarter I than those of small fish in both Quarters I and II suggests that the latter is the case. Based on these criteria first maturity of striped marlin occurred in the 155-165 cm length classes and in the 160-165 cm length classes of sailfish (Fig. 7, 8, 9, 10).

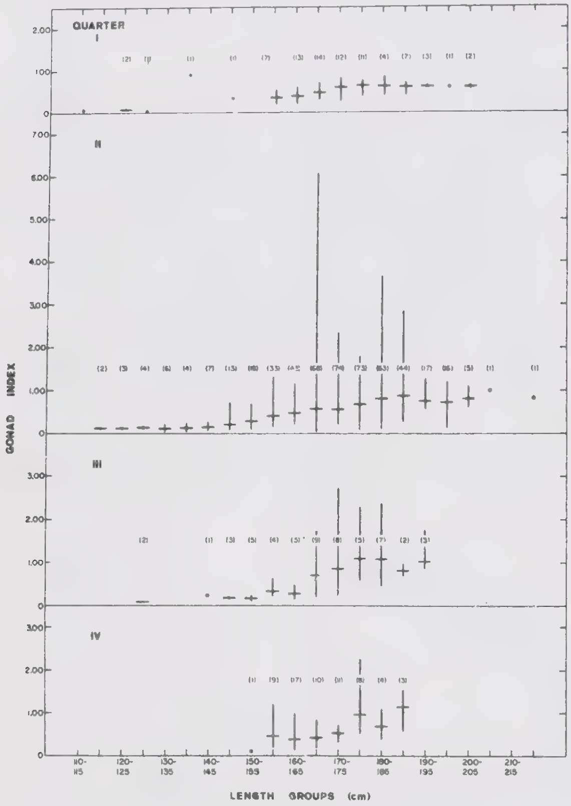

Figure 7.—Striped marlin gonad indices versus eye-fork length groups presented in quarters of the year. Numbers of striped marlin sampled are given in parentheses.

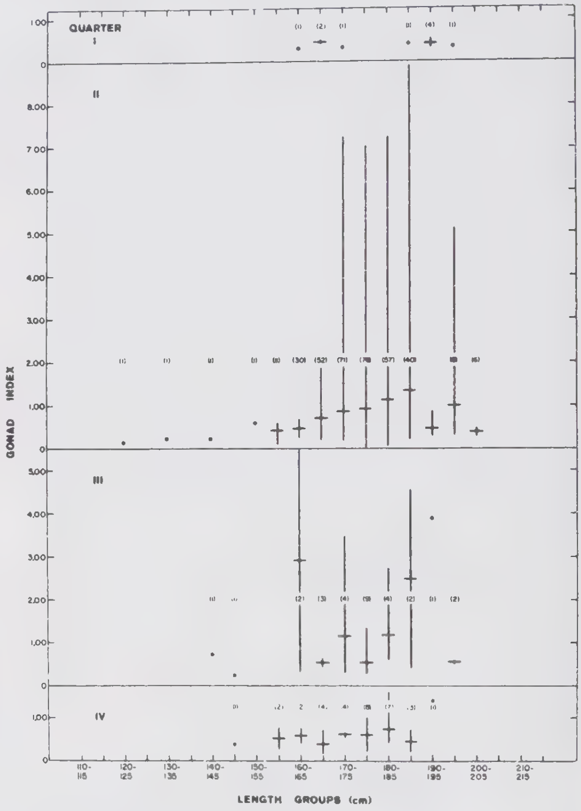

Figure 8.—Sailfish gonad indices versus eye-fork length groups presented in quarters of the year. Numbers of sailfish sampled are given in parentheses.

Frequency of Spawning

Simultaneous presence of both mature, nonatretic ova in the lumen and developing ova in the follicles is possible evidence of multiple spawning. However, lack of these conditions does not necessarily rule out multiple spawning. We plotted ova diameter frequency polygons of 300 ova from specimens with the highest gonad indices in each 2-wk period throughout 1969 and 1970. In addition, larger numbers of eggs were measured for one striped marlin and two sailfish, which had high gonad indices (Fig. 11). We found no indication of multiple spawning.

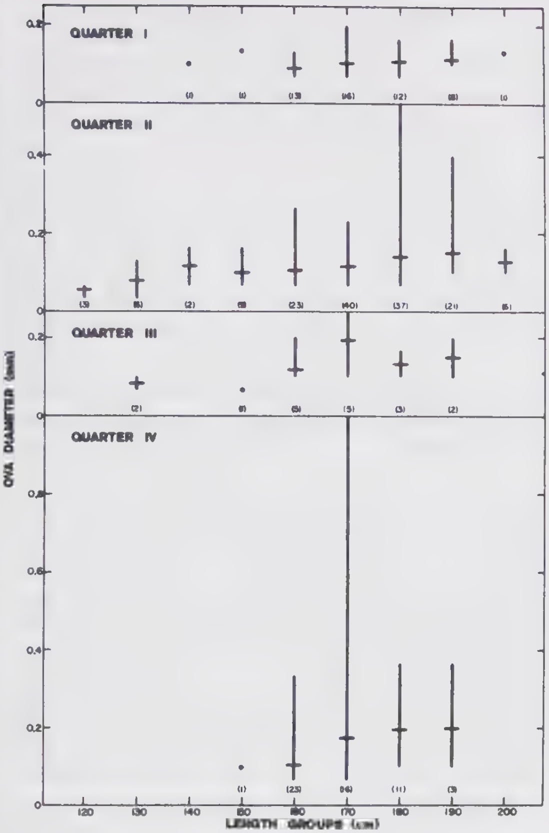

Figure 9.—Striped marlin ova diameters versus eye-fork length groups presented in quarters of the year. Numbers of striped marlin sampled are given in parentheses.

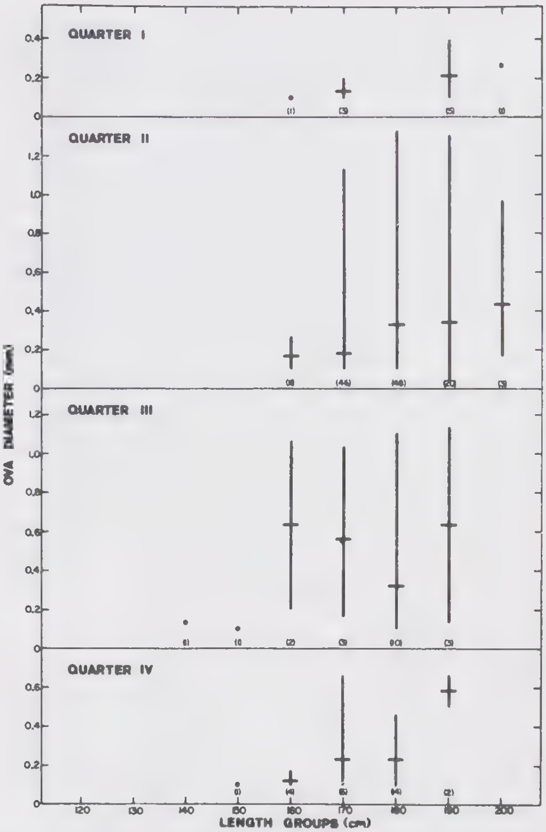

Figure 10.—Sailfish ova diameters versus eye-fork length groups presented in quarters of the year. Numbers of sailfish sampled are given in parentheses.

Fecundity

Little information is available on the fecundity of striped marlin or sailfish. Nakamura (1949) conservatively stated for billfishes in general that fecundity ranges from 1.0 to 1.2 million eggs depending on size and species. Merrett (1971) estimated a fecundity of 12 million eggs for an Indian Ocean striped marlin of 182 cm eye-fork length, with an ovary weight of 1.53 kg and a mean maximum egg diameter of 0.470 mm. In the central Pacific, Gosline and Brock (1960) estimated 13.8 million eggs for one striped marlin ovary.

We estimated the fecundities of four fully mature sailfish and three striped marlin by subsampling by weight. All specimens had high gonad indices and the striped marlin were specimens with the largest

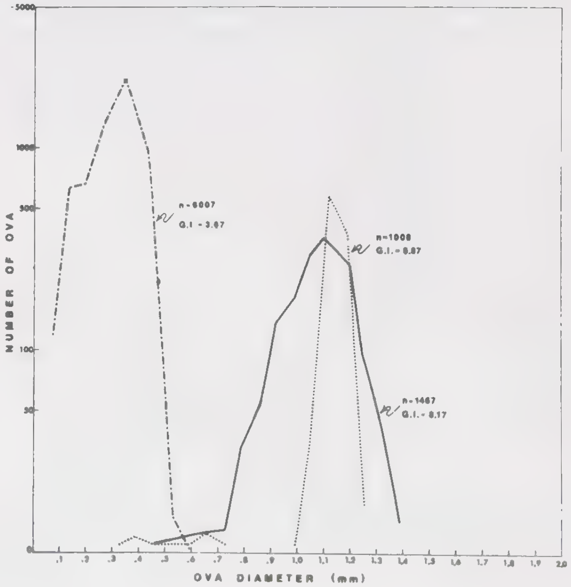

Figure 11.—Size frequency polygons for two mature sailfish (righthand curves) and one mature striped marlin.

ovaries encountered in this study. The fecundity estimates (Table 3) ranged from 11.3 to 28.6 million eggs for striped marlin and from 1.8 to 5.1 million eggs for sailfish.

Table 3.—Fecundity and related information on sailfish and striped marlin from the eastern North Pacific collected in 1969 and 1970.

	Gonad Index	Eye-Fork Length (cm)	Ovary Weight (gm)	Maximum Ova Diam. (mm)	Fecundity Estimate (million eggs)
Sailfish	3.7	185	2359	1.2	1.8
	5.5	163	2359	0.9	2.4
	7.0	176	3810	1.3	3.0
	8.9	187	5760	1.3	5.1
Striped Marlin	4.42	180	2580	0.6	11.3
	8.17	150	2760	0.6	17.2
	9.53	155	3550	0.6	28.6

Spawning Season and Locality

We are aware of only two publications that deal with spawning seasons of striped marlin and sailfish in the eastern Pacific (Kume and Joseph, 1969b and Yurov and Gonzales, 1972). Kume and Joseph (1969b) found that the highest frequency of striped marlin in spawning condition occurred in Quarter IV in the southern hemisphere and in Quarter II in the northern. Some were also in spawning condition in Quarter III in the northern hemisphere. These authors concluded that two spawning seasons existed at opposite times of the year in the northern and southern latitudes. This spawning pattern was also noticed in the western Pacific (Ueyanagi, 1959; Honma and Kamimura, 1958) and in the Indian Ocean (Williams, 1963; Merrett, 1971).

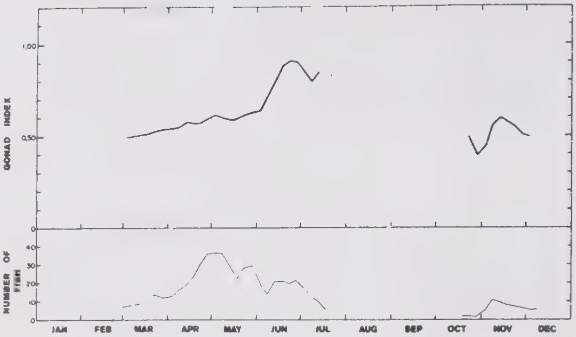

Figure 12.—Mean gonad index distribution and the number of striped marlin sampled by month from Buena Vista and Mazatlán.

Our data (Fig. 12 and 13) show a gradual increase

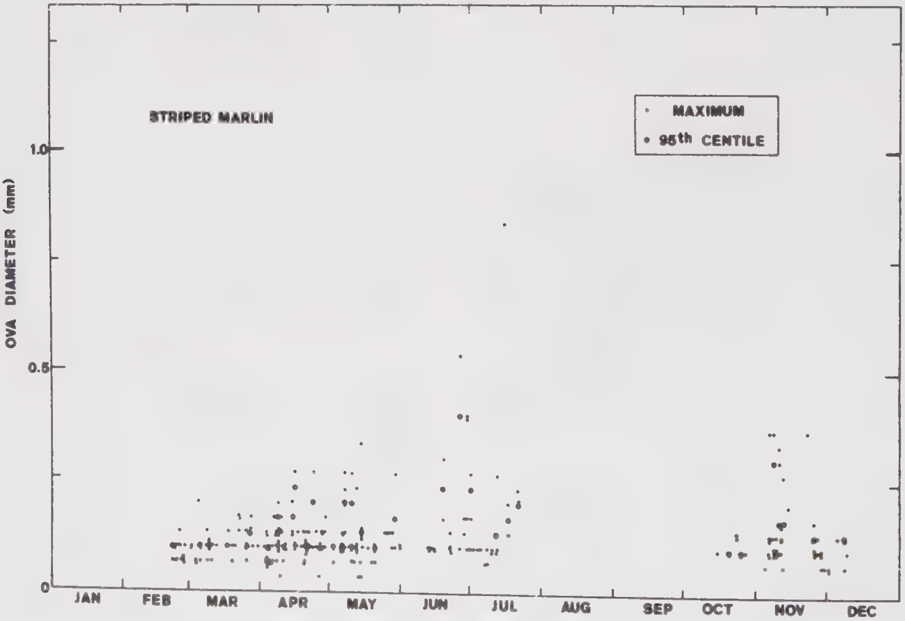

Figure 13.—Maximum ova diameter and 95th centile distributions by month from striped marlin ovaries sampled by Buena Vista and Mazatlán.

in maturation through June and July, at which time our sampling stopped. Several factors suggest that striped marlin move away from our sampling area at this time. Migration patterns indicated by Kume and Joseph (1969a) and Squire (1974b) showed that striped marlin move west-southwesterly from the coastal areas as the year progresses. Also, the data from the sport fishery (Fig. 2) show concentrations of striped marlin decreasing after March at Mazatlán and after July at Buena Vista. During July, Japanese longline fishermen have noted fully mature striped marlin in increased concentrations around the Revillagigedo Islands (G. Adachi, pers. comm.). The fish appeared in pairs and when one was hooked the other would remain alongside until the fish was hauled aboard. This behavior was not noticed in other areas of the eastern North Pacific or during other times of the year. Ovaries provided to us by the longliners from that area were all ripe and ranged in gonad index from 4.42 to 9.53 and the ova diameters were all in excess of 1.25 mm.

Sex ratio for striped marlin showed a slight but not significant predominance of males at Mazatlán from late February to July. In the larger and seasonally later catches at Buena Vista, males tended towards 60% from April through early June. The ratio then remained close to 50% into August. The October-early November ratios were also near 50%. Off San Diego, male striped marlin averaged only about 30% up to late September but rose to almost 50% for the rest of the season.

From these data it is logical to suggest that striped marlin migrate away from the coastal areas near the Gulf of California to spawn during July and possibly August. Females sampled at San Diego in August were in a post spawning condition and all had gonad indices less than 1.0.

Available evidence suggests that sailfish spawn nearshore in the eastern North Pacific with a northward progression of spawning activity during the year. Kume and Joseph (1969b) noted that some sailfish from Costa Rica coastal waters were in spawning condition from February to March. At the same time sailfish from offshore waters from lat. 0° to 15° were immature. Yurov and Gonzales (1972) reported spawning in the Gulf of Tehuantepec extending from February to April. We measured 36 larval and juvenile sailfish collected by Scripps Institution of Oceanography and the National Marine Fisheries Service along the Central American coast. Estimated spawning dates for these specimens based on back calculations using the growth rates of de Sylva (1957) indicated spawning of Costa Rican specimens from December through March, Guatemalan specimens mostly from January through April (with two in August), and Mexican specimens from April through November.

Our data conform to this pattern. Sailfish began to mature in late May and reached spawning condition in June and July (Fig. 14 and 15). The average gonad index showed a rapid decline in July, but this may be an artifact of a sharply reduced sample size. The ova remained large.

From April through July the sex ratio of Mazatlán sailfish remained close to 50%. Slightly more females than males were found until early June, after which time the ratio tended towards males. The smaller numbers of sailfish caught in Palmas Bay were predominantly female with males never exceeding 50%.

PARASITES

Among the incidental observations of parasites perhaps the most significant was the discovery of *Philichthys xiphiae* Steenstrup in the opercular bone in several striped marlin at Buena Vista and Mazatlán. Previously this species had been reported from the mucous canals of swordfish *(Xiphias gladius)* but not from any of the istiophorids and not from the eastern Pacific. The parasites were embedded in the preopercle just beneath the skin. The differences between parasitized and normal bones are readily seen in the x-ray photos in Figure 16. Other possible infection sites (bones) were not checked for this parasite nor were other billfish species.

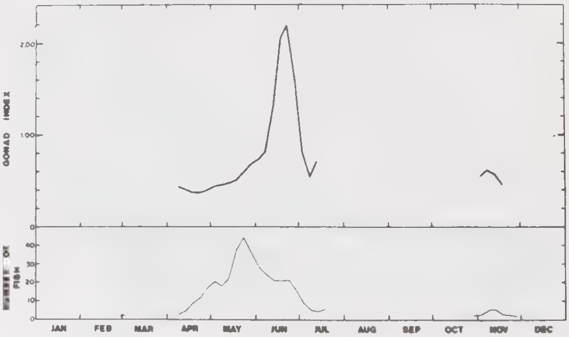

Figure 14.—Mean gonad index distribution and the number of sailfish sampled by month from Buena Vista and Mazatlán.

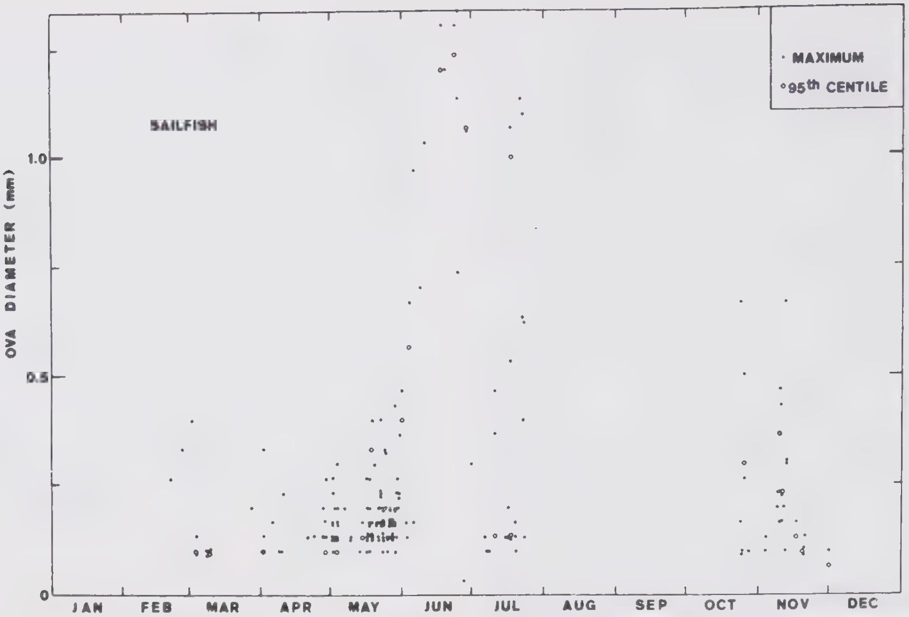

Figure 15.—Distribution of sailfish maximum ova diameters and 95th centiles by month from Buena Vista and Mazatlán.

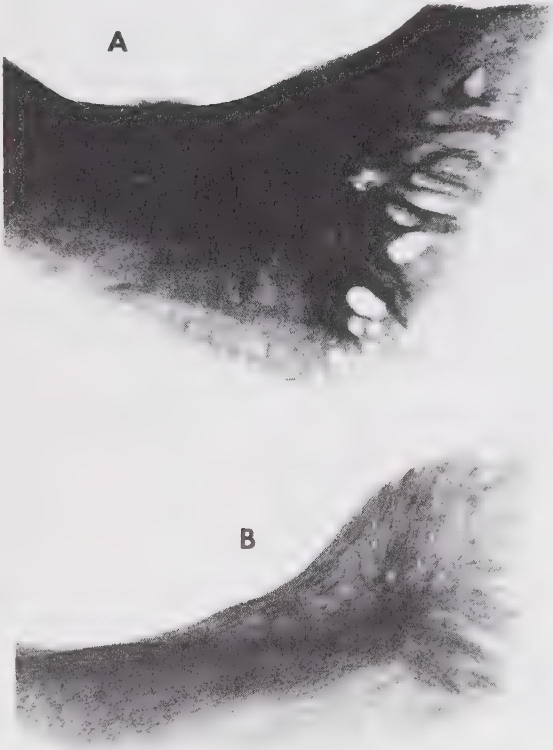

Figure 16.—X-ray photos of preopercular bones of striped marlin from Buena Vista showing (**A**) cavities caused by *Philichthys xiphiae* (**B**) a non-parasitized bone.

Caligoid copepods (some identified as *Pandarus* sp.) were common on the body surface and often very numerous, particularly in the ventral region just anterior to the anal fin. Large concentrations of these parasites appeared to irritate the skin, causing redness. White capsalid trematodes were commonly seen on the body surface. A different species of capsalid was found commonly in the nasal cavities. Isopods (some identified as *Nercila* sp.) were quite common on the body surface (usually on the fins) of sailfish at Mazatlán. Up to 57 isopods were recovered from a single sailfish. Nematodes were present, often numerous, in most of the billfish stomachs examined.

FOOD HABITS

Evans and Wares (1972) presented the data for 1967-1969. The contents of additional stomachs examined in 1970 (Table 4) are analyzed below. Table 5 presents the new data as percent occurrence and percent of total food volume. Table 6 compares the top ranked food items based on volume from the two studies. Except at San Diego, where the sampling dates were similar (August-October) in both studies, the comparison is between seasons as well as between years. The 1970 sampling in Mexico was from October through December whereas most of the earlier data was gathered from April through July.

The major departures from the results found in the previous study were the low importance of anchovies in San Diego striped marlin and of squid in Buena Vista sailfish stomachs.

Table 4.—Sample sizes and condition of billfish stomachs sampled during 1970.

	Striped Marlin			Blue Marlin	Sailfish
	SD	BV	Maz	BV	BV
No. Stomachs					
Total	37	59	8	15	33
With Food	20	37	4	8	22
Empty	16	5	1	2	2
Regurgitated	1	17	3	5	9
Total Vol. of Food (ℓ)	7.35	8.25	0.97	1.86	6.83

ACKNOWLEDGMENTS

We are indebted to representatives of resorts and clubs who permitted us to examine specimens of billfishes: Col. Eugene Walters, proprietor of Rancho Buena Vista; Bill Heimpel, proprietor of the Star Fleet at Mazatlán; Lois Ibey, Secretary of the San Diego Marlin Club. We are grateful to Lic. Ricardo Garcia Soto, Director of the Departamento de Tourismo de Baja California Sur for making available the reported catch data of sportfishing resorts in Baja California. We are also grateful to the managers of the following Baja California resorts for effort data: Bahía de Palmas, Rancho Buena Vista, Hotel Palmilla, Hotel Cabo San Lucas and Hacienda Cabo San Lucas. Several fleets at Mazatlán kept records of catch and effort for us and special thanks are due Bill Heimpel for his efforts. Other members of our staff who helped us collect and analyze the data were: Larry Coe, Dan Eilers,

Table 5.—Food species of billfishes observed in 1970 (% Occurrence/% Volume).

	Striped Marlin			Blue Marlin	Sailfish
	SD	BV	Maz	BV	BV
ALGAE	7.5/0.5	—	—	—	—
INVERTEBRATES					
Crustacea					
Decapods	—	3.0/0.2	—	—	—
Cephalopoda					
Argonauta sp.	—	—	50/6.2	—	—
Squid	5.0/0.4	62/24	25/1.2	13/1.1	12/3.1
FISHES					
Elasmobranchs	2.5/T	—	—	—	—
Clupeidae					
Etrumeus teres	—	43/39	—	—	18/24
Sardinops sagax	5.0/3.1	—	—	—	—
Opisthonema sp.	—	—	—	—	2.0/0.3
Engraulidae					
Engraulis mordax	2.5/2.2	—	—	—	—
Myctophidae	—	3.0/0.7	—	—	2.0/0.5
Scomberesocidae					
Cololabis saira	7.5/23.8	—	—	—	—
Atherinidae					
Atherinopsis californiensis	2.5/16	—	—	—	—
Exocoetidae					
Cypselurus californicus	2.5/0.2	—	—	—	—
Unidentified sp.	—	—	—	13/0.4	—
Fistularidae					
Fistularia sp.	—	—	—	—	8.2/21
Syngnathidae	—	—	25/0.4	—	—
Echeneidae					
Remora brachyptera	—	—	—	12/1.6	—
Carangidae					
Caranx caballus	—	3.0/0.8	—	—	2.0/0.6
Decapterus hypodus	—	3.0/1.7	—	—	2.0/4.4
Hemicaranx sp.	—	5.0/1.0	—	—	—
Trachurus symmetricus	38/62	—	—	—	—
Unidentified sp.	—	3.0/1.2	—	—	8.2/1.0
Coryphaenidae	—	—	—	—	2.0/10
Scorpidae					
Medialuna californiensis	5.0/2.4	—	—	—	—
Chaetodontidae	—	—	75/12	—	—
Mugilidae					
Mugil cephalus	—	—	25/79	—	—
Sphyraenidae					
Sphyraena sp.	—	3.0/2.3	—	—	—
Scombridae					
Auxis thazard	—	3.0/0.4	—	37/36	6.1/13
Euthynnus lineatus	—	5.1/17	—	12/19	8.2/13
Sarda chiliensis	2.5/0.8	—	—	—	—
Scomber sp.	—	3.0/2.1	—	—	4.1/2.3
Unidentified sp.	—	—	—	25/39	—
Balistidae					
Balistes sp.	—	3.0/0.1	—	—	6.1/0.4
Tetraodontidae					
Sphoeroides sp.	—	3.0/2.2	—	—	—
Lagocephalus lagocephalus	—	19/6.4	—	—	10/4.0
Unidentified Fish	20/3.9	8/1.4	50/1.4	38/2.2	6.1/1.4

Table 6.—Comparison of major billfish foods in 1970 with those for 1967-1969 (n = no. of stomachs with food).

	STRIPED MARLIN				
	1967-1969			1970	
	Rank	Species	%Vol.	% Vol.	Species
San Diego		*n* = 116			*n* = 20
	1.	*Engraulis mordax*	60	62	*Trachurus symmetricus*
	2.	*Trachurus symmetricus*	27	16	*Atherinopsis californiensis*
	3.	*Cololabis saira*	5	8	*Cololabis saira*
Buena Vista		*n* = 303			*n* = 37
	1.	Squid	49	39	*Etrumeus teres*
	2.	*Etrumeus teres*	30	24	Squid
	3.	*Scomber japonicus*	7	17	*Euthynnus lineatus*
	4.			6	*Lagocephalus lagocephalus*
Mazatlán		*n* = 14			*n* = 4
	1.	Squid	63	79	*Mugil cephalus*
	2.	*Argonauta* sp.	7	12	*Chaetodon* sp.
	3.	*Balistes* sp.	7	6	*Argonauta* sp.
	4.	*Fistularia* sp.	5		
			SAILFISH		
Buena Vista		*n* = 14			*n* = 22
	1.	Squid	35	24	*Etrumeus teres*
	2.	*Etrumeus teres*	29	21	*Fistularia* sp.
	3.	*Fistularia* sp.	22	14	*Euthynnus lineatus*
	4.	*Naucrates ductor*	7	13	*Auxis thazard*
			BLUE MARLIN		
Buena Vista		No Data			*n* = 8
	1.			39	Scombrids (unidentified)
	2.			36	*Auxis thazard*
	3.			19	*Euthynnus lineatus*

Douglas Evans, Stewart Luttich, Howard Ness, and David Tolhurst. Roger Cressey identified *Philichthys xiphii* and Ernest Iversen identified the parasites *Pandarus* sp. and *Nercila* sp.

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MFR PAPER 1060

Success of the live-bait tuna
fishery rides on the success
of the fishery for bait.

Some Considerations of the Problems Associated with the Use of Live Bait for Catching Tunas in the Tropical Pacific Ocean

FRANK J. HESTER

ABSTRACT

This report provides a summary of tropical Pacific tuna live-bait fishing methods, identifies the major problems restricting the expansion of live-bait fisheries in the Pacific, and gives references and suggestions on methodology to investigators interested in working on baitfish problems.

INTRODUCTION

The use of live bait to catch tunas, called baitfishing in the eastern Pacific and pole-and-line fishing in the central and western Pacific, has been described by a number of authors (Godsil, 1931; June, 1951; Iwasaki, 1970; Isa, 1972; and Webb, 1972, 1973). The method probably was developed to its highest form in Japan from whence it spread, with modifications, across the Pacific and into the Atlantic during the first part of the 20th century.

The 1971 world tuna landings were 1,150,000 metric tons (FAO, 1971). Of this total catch, baitfishing accounted for about 244,000 metric tons (21%), purse seining took 228,000 metric tons (20%), and longlining took 427,000 metric tons (37%). The remaining 251,000 metric tons (22%) of tunas were taken by a variety of methods such as trolling, and traps and weirs, or were caught by the three principal methods but could not be so identified from the statistics.

For a description of tuna purse seining see McNeely (1961) and Green, Perrin, and Petrich (1971), and for tuna longlining, Shapiro (1950).

Live-bait fishing for tunas depends upon quantities of suitable baitfishes, which are used to attract schools of tuna to the boat and to excite them into a feeding mode so that they can be caught by lure and a pole and line. The principal tuna species taken with baitfishes are skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares*; and albacore, *T. alalunga*. The live-bait albacore fisheries are in temperate waters. The discussion of live-bait tuna fishing in this paper will be limited to the tropical tunas—yellowfin and skipjack. Five elements of baitfishing for tunas will be reviewed and discussed: types of bait, catching the bait, holding and transporting the bait, fishing the tuna schools, and bait supply.

TYPES AND CHARACTERISTICS OF A GOOD BAITFISH

In order to be a suitable live bait, the baitfish must be of a size and appearance acceptable to the tunas, its behavior must be such that the tunas are attracted to the boat and induced to bite, and the bait must be sufficiently hardy to remain alive during capture and transport. In this regard resistance to mechanical damage, i.e., loss of scales and bruising, is important, as is the bait's tolerance to temperature and temperature change so that the bait can be carried by the fishing boat from one fishing ground to another through waters of varying temperatures.

The preferred baitfishes for tuna fishing are clupeoids, principally the anchovies and their relatives. The clupeoids in general are good baits, being of the proper size (25-100 mm) and possessing the silvery appearance and the behavior that induces feeding behavior in the tuna. These fish are active swimmers that do not disperse when thrown into the water but maintain a semblance of schooling behavior and do not swim away or dive deep but stay close to the vessel.

When suitable supplies of clupeoids

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Table 1.—Effectiveness of live bait.

Area and period	Bait species	Unit of measure	Quantity	Tuna catch (metric ton)	Effectiveness Kilogram bait/ metric ton tuna
Japan, 1968[1]	Anchovy, *Engraulis japonicus*	Bucket ≈ 5.5 kg	4.4×10^6 buckets	168×10^3	143.0
Japan, 1971[2]	do	Bucket ≈ 5.5 kg	250 buckets 1,375 kg	71.9	19.4
Hawaii, 1965-71[3]	Anchovy (nehu), *Stoliphorus purpureus*	Bucket ≈ 3.5 kg	34×10^3 buckets 0.8×10^6 kg	4.5×10^3	28.50 $S^2 = 51$ (variance)
Eastern Pacific, 1948-59[4]	Anchoveta, *Cetengraulis mysticetus*	Scoop 4.1 kg	3.5×10^6 scoops 14.5×10^6 kg	114×10^3	128.1 $S^2 = 783$
Eastern Pacific, 1960-69[4]	do	Scoop 4.1 kg	0.41×10^6 scoops 1.7×10^6 kg	23×10^3	68.2 $S^2 = 158$
Palau Islands, 1966[5]	Anchovy (nehu), *Stolephorus heterolobus*	Bucket ≈ 3.5 kg	62.7×10^3 buckets 0.22×10^6 kg	2.9×10^3	87.4 $S^2 = 1008.8$
Ryukyu Islands, 1967[6]	Mixed—predominantly apogonids and lutjanids	Kilogram	0.27×10^6 kg	5.1×10^3	52.6
Hawaii, 1962[7]	Tilapia, *Tilapia mossambica*	Not available	Not available	Not available	≈ 60
Hawaii, 1968[8]	Shad, *Dorosoma petenense*	Bucket ≈ 3.5 kg	56 buckets 176 kg	4.8	37
Hawaii, 1971[9]	Shad, *Dorosoma petenense*	Bucket ≈ 3.5 kg	204 buckets 728 kg	12.5	58
Hawaii, 1973[10]	Northern anchovy, *Engraulis mordax*	Bucket ≈ 3.5 kg	3 buckets 10.5 kg	0.7	15
Hawaii, 1973[11]	Golden shiner, *Notemigonus crysoleucas*	Bucket ≈ 3.5 kg	Not available	Not available	118

[1] Based on total anchovy bait catch and total home and southern waters landings of yellowfin tuna, skipjack tuna, and albacore. (Source: [Japan.] Ministry of Agriculture and Forestry. Statistics and Survey Division, 1970.)

[2] Based on average bait capacity and average catch per trip of southern waters vessels (Anonymous, 1971).

[3] Source: Hawaii Division of Fish and Game and Bumble Bee Seafoods (1970).

[4] Source: Inter-American Tropical Tuna Commission (1956, 1960, 1966, 1970). Note: From 1960 on most of the large bait boats converted to purse seiners and left the bait boat fleet.

[5] Source: Congress of Micronesia (1972).

[6] Source: Isa (1972).

[7] Source: Shomura (1964). Quantity and weight of bait not given. Results are based on average catch rate comparison with nehu, nehu being considered to have an effectiveness of 30.

[8] Source: Iversen (1971).

[9] Source: Iversen, R. T. B. 1973. Commercial fishing for skipjack tuna with threadfin shad as bait. Unpublished report, 4 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[10] Source: Uchida, R. N., Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. comm.

[11] Source: Kato, K., Fishfarms Hawaii, P.O. Box 898, Kihei, HI 96753, pers. comm.

are not available, bait boats, especially those operating in island areas, resort to the use of any proper-sized fishes that can be obtained in reasonable quantity including a wide variety of tropical reef fishes such as juvenile mullets, Mugilidae; goatfishes, Mullidae; cardinalfishes, Apogonidae; damselfishes, Pomacentridae; silverside, Atherinidae; snapper, Lutjanidae; mosquitofish, Poeciliidae; rabbitfish, Siganidae; etc.

Baitfish acceptability is determined by three factors: supply, which is discussed in a separate section of this report, mortality, and effectiveness. Live bait is subject to continuous loss from the time it is obtained to the time that it is used for fishing. Strong bait, that is bait that survives capture and holding well, is in great demand. Studies of factors affecting mortality have been made by Baldwin, Struhsaker, and Akiyama (1971), and Anonymous (1971). Bait mortality is a complex problem and needs much additional work, particularly in connection with long distance transport and holding of large quantities of bait.

Effectiveness, that is the production of tuna per quantity of bait, is difficult to quantify owing to lack of good statistics on bait usage. From Table 1 it is apparent that there is a wide range of effectiveness expressed in kilogram bait per metric ton of tuna produced. The smaller the ratio the more effective the bait. These measures of effectiveness are subject to several biasing errors that result in an overestimate of the bait needed. The largest error is due to the use of total bait caught rather than bait used in fishing. Thus mortality is included in these estimates.

Also included is bait dumped when fishing is completed.

Sources of error that affect the variance of the estimates are the size of the tuna fished, more bait being required to take a ton of small tuna, the reporting of bait catches by the bucket or scoop, the constancy of which is questionable, and the complex relation between bait mortality and time spent looking for fish. The latter may account in part for the increase in effectiveness in the eastern Pacific fishery after 1960 when the bigger boats dropped out of the fishery leaving as the principal users of bait the smaller boats that perhaps did not spend as much time scouting for tuna.

BAIT CATCHING METHODS

Baitfishes are caught by several types of gear, the most common being the bait seine. The details of this type of gear and operation vary from locality to locality. In Hawaii the so-called day net, a round-haul net for shallow water that lacks wings, bag, or purse line, is used. The dimensions for a typical day net are 175 by 4 m constructed of 4.8 mm stretched mesh webbing (Figure 1). The main bait species taken is the nehu, an anchovy, *Stolephorus purpureus*, which is quite small and requires a small-meshed net. Another common bait net, used chiefly in the eastern Pacific, is the lampara, which has wings and a bag section, is deeper, and can be used in waters where the leadline does not necessarily maintain contact with the bottom. Details of the operation using this gear are given by Scofield (1951) and Du Plessis (1959).

For baiting in deep water, the purse seine is effective, being superior to the lampara but requiring more manpower. For shallow water areas where the bottom is too rough to drag or walk the leadline of the net, the drive net is used (Figure 2).

> "The 'drive-in-net' fishing method is said to have been developed in the Ryukyu Islands (Shapiro, 1949) to catch shoaling fishes in coral reef areas. Divers, sometimes carrying fish-chasing devices, drive the fish school into a net set strategically to block the path of the fish. As soon as the fish are driven into the net, the net is lifted to the surface. This method has long been used for catching mainly the Apogonidae and Caesionidae. The size and design of the net differ according to the fish to be captured. The net usually consists of a bunt and two wings when catching larger and faster swimming fishes such as adult *Caesio*, flyingfish, and garfish. Only the bunt of the net or a blanket net is used for catching apogonids or other slower swimming fishes or juvenile fishes. The drive-in net is used to capture apogonids early in the morning by taking advantage of their nocturnal habit. The bait fishermen cover a reef with the net before sunset. The fish are found hiding in crevices. The net is allowed to remain overnight. The opening over the crevice in which the fish are hiding is kept open in order to enable the fish to move out at night. The fishermen catch the baitfish early in the morning by driving the fish into the net before the fish can return to their hiding places.
>
> "The fishermen also catch the apogonids during the day by inserting tree leaves into crevices and scaring them out. Some apogonids are observed during the day with other baitfish and are caught along with them. The red scads (*Caesio*) and 'blue bait' are caught during the day." Isa (1972).

A second type of baiting operation is night baiting, commonly used in coral-island areas. In this operation a strong underwater light, 750-1,500 w, is submerged to as deep as 20 m below the surface and allowed to remain until a quantity of bait has been attracted. The light then is slowly drawn up toward the surface near a net suspended vertically in the water. The net typically is of 6.4 mm mesh and nearly square, being about 25 m on a side. Once the light and bait are at the surface, the net is raised under the bait (Figure 3). For details of this method see June (1951).

Catching bait for tuna fishing is dependent primarily on the availability of quantities of bait and not on the lack of a suitable method of taking them; i.e., the methodology

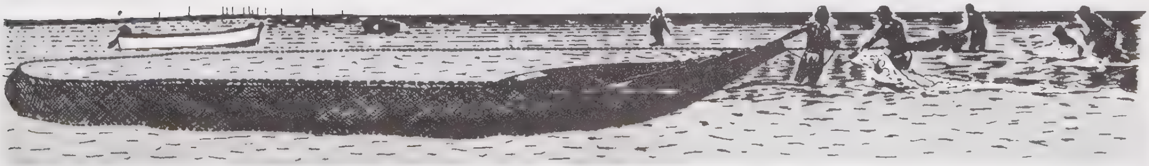


Figure 1.—Hawaiian-type day net being set on the reef for iao, a small atherinid.

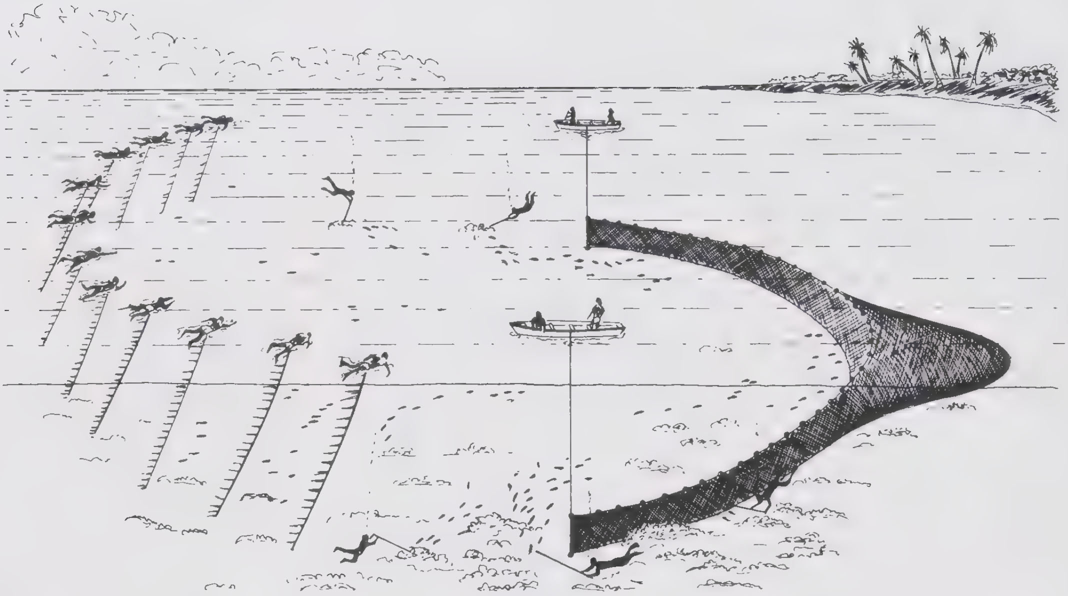


Figure 2.—Catching bait with a "drive-in" net.

has been well worked out and usually presents a minor problem to a bait boat. However, there are some exceptions. These include the introduction of, or the learning of, methods suited for certain areas by fishermen from other areas. For example, the Okinawan live-bait fishermen are generally believed to be the best or most knowledgeable for operating in coral island areas where they manage to find and take bait when fishermen from Japan or the United States would fail. In part their success lies in the use of wall nets (Isa, 1972) suspended near coral heads or close to drop-offs. Also, they are adept at the swim-in method of bait catching (*ibid*.). Even when more desirable baits are absent they are able to take small quantities of bait by tearing apart coral heads. This practice is not to be recommended but is used at times. Species taken in this manner include small damselfish and cardinalfish.

A source of bait that might be used if the catching techniques could be developed occurs offshore where schools of clupeoids and carangids exist in considerable abundance and sometimes come to a light. Also it is frequently observed that floating objects attract quantities of small fish, and it may be that natural or artificial floating "logs" together with a lampara or purse seine might be used to obtain bait. It may be possible to develop a night-light, lift-net operation or a deepwater lampara or seine operation that could provide supplies of offshore bait at certain times in certain places. Night baiting using deeply submerged lights either inshore or offshore is undergoing further refinement in some areas. In addition, the use of set nets, or weirs, may hold promise in areas where the bait species are migratory either along the shore or inshore-offshore.

HOLDING AND TRANSPORT OF THE BAIT

Once the bait is in the net, it must be transferred to holding tanks or wells (eastern Pacific and Japan, Figure 4) or "boxes" (central-western Pacific) aboard the vessel or into receivers if it is not to be loaded on the vessel immediately. When the baitfishes are hardy, as is the case with most of those taken in the eastern Pacific, the transfer from the net to holding tanks or receiver is accomplished with a dip net or scoop. In the 1950's at the height of the bait boat era in the eastern Pacific a scoop held about 4 kg of bait and was the common unit of measure used. Today with the trend towards smaller bait boats the scoops are smaller and hold 1-2 kg. Elsewhere, where the bait species are more delicate and subject to high mortality by abrasion and bruising (the tropical clupeiods with their highly deciduous scales are particularly susceptible), the transfer is made by the use of buckets. These are generally of seamless stainless steel with a capacity of about 15 liters. The bucket keeps the fish mixed with sufficient water to reduce scale loss and bruising. In areas such as Hawaii and Japan, the bucket is the common unit of measure for baitfishes. The bucket holds on the average 3.5 kg of bait in Hawaii and 5.5 kg of bait in Japan although, as with the scoop, the actual amount is quite variable.

Injury and shock during transfer of the bait into the holding tanks or receivers account for most of the mortalities. Losses can be very high if the bait has been handled carelessly. Bucketing appears to reduce mortality as does increasing the amount of oxygen in the holding tanks, reducing the temperature, lowering salinity, and avoiding crowding and undue excitement of the bait until it has had a chance to acclimate to its new environment. For discussion of ways of reducing the rate of mortality associated with the Hawaiian live-bait fish nehu, *S. purpureus*, see Baldwin et al. (1971). In addition, methods of avoiding brailing or bucketing bait from the net to the wells could stand closer examination. For example, the swim-aboard technique used by the west coast bait haulers might be adapted to commercial baitfishing operations. This is a method where the fish enter the well through a gate at the waterline of the vessel thereby avoiding the brailing operation.

Some work has been done in transferring bait by means of pumps (Baldwin, 1969). Whether or not this

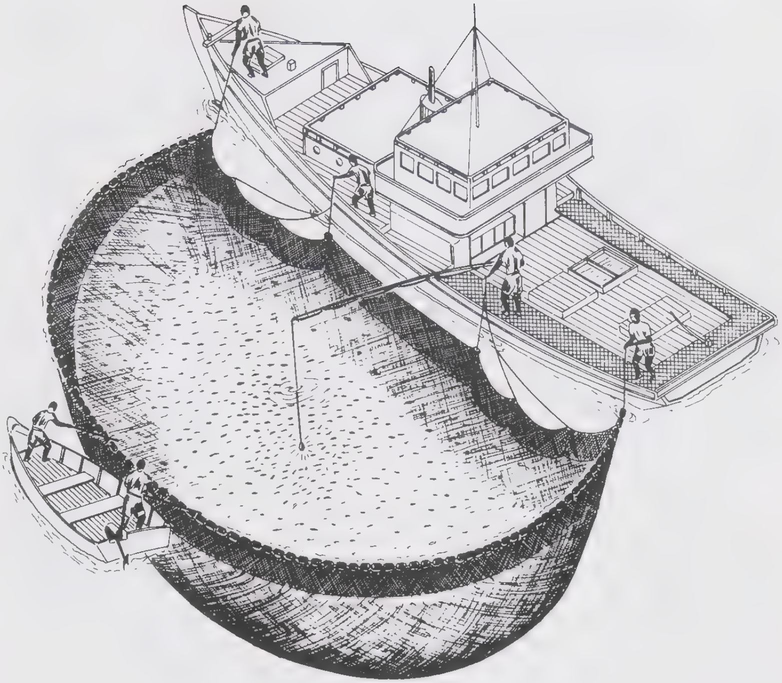


Figure 3.—Night baiting with a Hawaiian-type lift net.

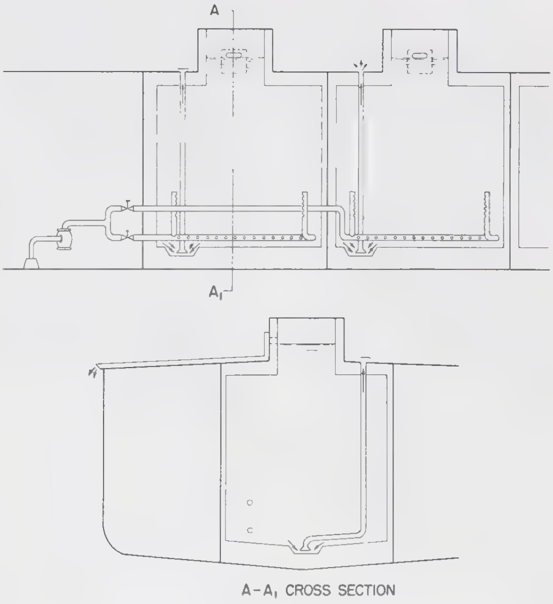
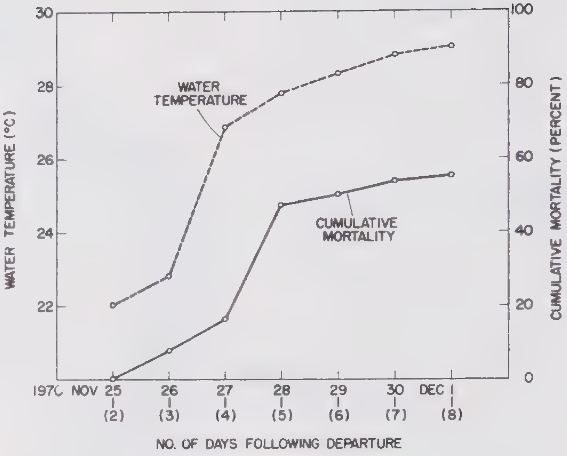


Figure 4.—Japanese bait boat wells showing the perforated inflow pipe, overflow, and "bilge"-pipe for continuous removal of dead bait. (From Miho Shipbuilding Co., 1966.)

Figure 5.—Relation between water temperature and bait mortality on a vessel traveling from Japan to the southern water gounds. (From Anonymous, 1971.)



would result in reduced mortality is open to investigation. It certainly would speed up the loading operation.

In holding baitfish aboard vessels, there are a number of factors that are important. First is the supply of water. In the central and western Pacific with the older Japanese, Hawaiian, and Okinawan style vessels, water comes in through holes in the boat at the bottom of the boxes, circulation being assured either by the motion of the vessel through the water or the rolling of the vessel by wave action. The amount of oxygenated water supplied in this manner is adequate for small quantities of bait held for short periods. With the vessels of the eastern Pacific and the newer Japanese pole-and-line vessels that carry large quantities of bait over great distances, circulating seawater is supplied by pumps to the wells. As a general rule, a turnover of the water in the wells 5 to 10 times an hour is desirable. Typically, a 10-m^3 well would have a water exchange at the rate of about 1,500 liters per minute. The carrying capacity of a well with forced circulation varies from 10 kg of baitfish per cubic meter of water to as high as 50 kg per cubic meter. Capacity is affected by water temperature (Figure 5), the species and condition of the bait, and the sea state, high mortality of the baitfish occurring during rough weather. Proper lighting in the wells also is an important factor in reducing mortality.

If the bait is to be maintained for an extended period of time it is necessary to feed it. This is a problem particularly in the eastern and western Pacific where large bait boats will try to keep bait aboard for several weeks. Foods used vary from chopped fish to bread and meal and prepared fish chows.

It is important that the bait be rested before the trip begins. This is frequently done by holding the bait in receivers or in the tanks for several days prior to departure from the baiting grounds. In the Japanese southern water fishery, for example, where the vessels transport their bait from Japan to the tropical western Pacific, the bait is rested in receivers for several weeks prior to departure.

Another source of mortality that can present a problem in the central and western Pacific occurs when the bait comprises a mixture of species. If the mixture involves larger predatory fish together with the smaller desirable bait species, the larger predators will either eat or frighten the bait resulting in a high mortality. Also not uncommon are instances where juvenile lae, *Scomberoides sancti-petri*, a small carangid, is taken with the bait and causes high or complete mortality by biting the scales off the baitfish (Struhsaker, Baldwin, and Murphy, unpublished[1]). Development of satisfactory separators to separate the desirable from the undesirable species needs investigation.

For chumming, the baitfish are crowded with a small net or "crowder" so that they can be easily brailed out. With some species this causes an extreme fright reaction and high and rapid mortality. The sprats, *Spratelloides* sp., called piha in Hawaii, are plentiful and ubiquitous throughout the central and western Pacific. However, these are very delicate baitfish that die within a few hours of loading into the well. In part the mortality occurs during crowding for chumming and if this mortality could be alleviated, these plentiful fishes would represent a major increase in bait supply throughout the island areas.

A so far neglected area for investigation is the use of drugs to lessen the fright reaction and metabolic requirements of baitfishes. For example, the use of anesthetics and tranquilizers in the transport of trout, salmon, and other freshwater fish is more or less routine, whereas this is not the case in the transport and holding of marine baitfishes.

FISHING OPERATIONS—CHUMMING

Baitfishing for tunas depends upon locating surface tuna schools. Once the school is located, a portion of the bait in the well is crowded with a net into a reduced area where it can be dipped out with a dip net. Small amounts of bait are tossed into the water in such a way as to bring the tuna to the boat. Chumming techniques vary somewhat with area and with the type and quantity of bait available. Various tricks are used to alter the behavior of the bait to make it attractive to the tunas. A good chummer has techniques that produce tuna at a rate that an inexperienced chummer cannot match.

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[1] Struhsaker, J. W., W. J. Baldwin, and G. I. Murphy. n.d. Environmental factors affecting stress and mortality of the Hawaiian anchovy *(Stolephorus pupureus)* in captivity. n.p. Completion report prepared for National Marine Fisheries Service under Commercial Fisheries Research and Development Act (P.L. 88-309), Project H-10-R. Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744.

The handling of the boat varies with area, too. In the eastern Pacific and in Hawaii the vessel moves slowly ahead and fishing is conducted from the stern. In the Japanese- and Okinawan-type fishing the vessel is stopped dead in the water and fishing is conducted along one entire side from the stern to the end of the extended bowsprit. The crewmen aboard Japanese- and Okinawan-style boats generally number 3 to 5 times the men aboard a Hawaiian- or west coast-style bait boat. Production figures per day's fishing between the two methods are generally comparable, however. It is believed that the use of bait by the eastern Pacific boats is more profligate than by the Hawaiian or oriental boats and indeed there appears to be some truth to this belief (Table 1). However, the number of baitfishes thrown per school is probably near equal owing to the different size of the fish used. Good data are not available for the Japanese southern water fishing vessels.

It is interesting to note that the use of a water spray system (Yuen, 1969) throughout the central and western Pacific is absent or very uncommon in the eastern Pacific. Whether or not the vessels would be more productive in the eastern Pacific if water sprays were used is not known, but comparison between fishing with and without the water spray shows that it indeed does affect the catch rate in Hawaiian waters (*ibid.*).

SUPPLY

The major problem in baitfishing is obtaining a sufficient and dependable supply of bait. Discussed in this section will be natural bait, rearing of bait, transport of bait, and artificial bait. The introduction and establishment of nonendemic bait species will not be considered. Pertinent to any discussion of supply is the question of the value of the bait to the fishermen. How much is it worth to the fishing operation to have bait aboard? Obviously without bait there can be no production of tuna and therefore no income. A number of studies have been undertaken in order to assign some value to the bait. The methodology used includes the empirical approach, the examination of what fishermen are willing to pay for bait available for sale; the opportunity cost approach, what catching bait costs the vessel in terms of lost fishing time; and the marginal product approach, a method that gives a maximum value for bait.

Live bait is sold to commercial fishing operations in Japan and to a lesser degree on the west coast of the United States. In the case of the former, the vessels pay about $10 per bucket ($2 per kg) at the bait seller's receiver. The bait then has to be transported to the fishing grounds and may undergo considerable mortality, typically 20% to 30% but at times much higher. On the west coast of the United States the selling price of bait may be as low a $2 per scoop ($0.50 per kg), the amount of bait in the scoop being less than the Japanese bucket. Again, the buyer has to accept the mortality during transport from the bait seller to the fishing grounds. During a recent experiment where northern anchovy, *Engraulis mordax*, was brought in from California to Hawaii, the vessels were willing to pay $20 per bucket.

With the exception of Japan it appears to be more traditional for each vessel to carry its own bait net and bait skiff and to catch its own bait. Under these circumstances it is possible to estimate the cost of catching the bait based on the time lost to fishing. For example, in Hawaii, studies suggest that between 25% and 30% of the time available for fishing is spent searching for and catching bait. This puts the cost per bucket of bait between $12 and $30 ($3.50 and $8.50 per kg) (Brock and Takata, 1955; Shang and Iversen, 1971). Similarly studies in Hawaii based on the production function method suggest that the value of a bucket of bait is as high as $80 ($23 per kg) to the vessel (Elliott, Keala, and Matsuzaki, unpublished[2]). Because of the wide range among these figures, for planning purposes a good estimate is $10-$20 per bucket ($3-$6 per kg). It is questionable whether refining these cost estimates is worthwhile at this point since the sociological problem of convincing fishermen to purchase bait appears to be greater than convincing them that the bait is worth so many dollars per bucket based on their fishing operation. Past experiments for example whereby the State of Hawaii raised tilapia, *Tilapia mossambica*, for bait (Brock and Takata, 1955; Shomura, 1964) and made it available to the vessels at a nominal price failed, not because the price of the bait was too high but because the fishermen felt that the bait they could catch was superior and free. Since then their attitude towards the purchase of bait has changed to a great degree.

Natural Bait Supplies

The location of abundant natural baits (Table 2 and Figure 6) is of prime concern for the expansion of bait fisheries in the central and western Pacific. The location of bait usually depends upon bait surveys, which

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[2] Elliott, D. P., B. A. Keala, and C. Matsuzaki. n.d. Estimation of demand for live bait to be used in the skipjack fishing industry. 21 p. [Technical report submitted to Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.]

Table 2.—Availability of bait for live-bait fishing in the Pacific and Indian Oceans.

Area[1]	Kinds of baitfish	Commercial landings	Used for live bait	Potential
1 Indian Ocean	Anchovy, sardine, herring	>100,000 metric tons	?	Very good
Minicoy, Laccadive Is.	Reef fishes—apogons, damsels, etc.	Limited amount	Yes	Limited, small fishery
2 Southeast Asia	Anchovy, sardine, herring	>40,000 metric tons	?	Very good
3 Japan: Northeast	Anchovy, *Engraulis japonicus*	7,299 tons	1,970 tons	Excellent
Central	do	73,541 tons	10,857 tons	Excellent
Southwest	do	144,508 tons	11,200 tons	Excellent
4 Formosa[2]	Anchovy	?	?	?
5 South Korea[3]	Anchovy	?	?	?
6 Philippine Is.	Anchovy	20,000 metric tons	?	Very good
7 Marianas	Rabbitfish, etc.	?	?	Very poor (highly seasonal)
8 Western Carolines	Anchovy, sardine, silverside, round herring, etc.	?	Est. >100,000 buckets	Good
9 Eastern Carolines	do	?	?	Poor, OK for small scale operation
10 New Guinea[4]	Anchovy, sardine	?	?	?
11 Fiji	Anchovy, sardine, silverside, mackerel, etc.	?	Experimental	Good
12 Solomon Is.[5]	Sardine	?	Yes	?
13 Gilbert Is.[6]	Sardine	?	?	?
14 Phoenix Is.	Goatfish, mullet, etc.	?	?	Poor
15 Marshall Is.	Sardine, silverside, round herring, etc.	?	Experimental	Good
16 Samoa	Sardine, anchovy, mackerel, etc.	?	Experimental	Poor
17 Society Is.	Mackerels, round herring, etc.	?	Experimental	Poor
18 Tuamotu Archipelago	Goatfish, mullet, round herring	?	Experimental	Poor
19 Marquesas Is.	Sardine	?	Experimental	Good (seasonal)
20 Line Islands	Goatfish, mullet, etc.	?	Experimental	Poor
21 Hawaii	Anchovy, silverside, round herring, etc.	?	ca. 35,000 buckets (130 metric tons)	Good
Leeward Is.	Silverside, mullet, goatfish, etc.	?	Experimental	Poor
22 Eastern Pacific: California to Panama	Anchovy, anchoveta, sardine	>200,000 metric tons	4,000,000 scoops (14,500 metric tons)	Excellent
23 Southeastern Pacific: Panama to Chile	Anchoveta	Est. 10,000,000 metric tons	600,000 scoops (2,200 metric tons)	Very good

[1] See Figure 6.
[2] The Japanese mention Formosa as a possible baitfish source.
[3] The Japanese mention Pusan as having a good supply of strong bait.
[4] The Japanese operate several boats in this area.
[5] The Japanese have 6 boats in this area; will increase to 11.
[6] The Japanese have been operating in the area

may give misleading results unless they extend over a long time span. Survey methods include full-scale catching operations, diver surveys, interviews with inhabitants, aircraft, beachwalking, etc. Examples of recent bait surveys are [Japan.] Fisheries Agency (1969), Hida (1971), Wilson (1971), and Kearney, Lewis, and Smith (1972). Problems with surveys include the seasonal or cyclic changes in abundance of species whereby certain areas that may have plentiful quantities of bait one day, may have none the next. Too, the amount of bait may vary from year to year or over a many-year period. Even when baitfishes are located in quantity, the question still arises as to the amount of bait that can be taken. Few if any population dynamics studies have been done on tropical bait species. Perhaps the most intensive involved the anchoveta in Central America (Bayliff, 1966), and a study of the tropical anchovies in Palau by Garth I. Murphy (University of Hawaii, Honolulu, HI 96822) is still in progress. Most of these fisheries appear to be capable of tol-

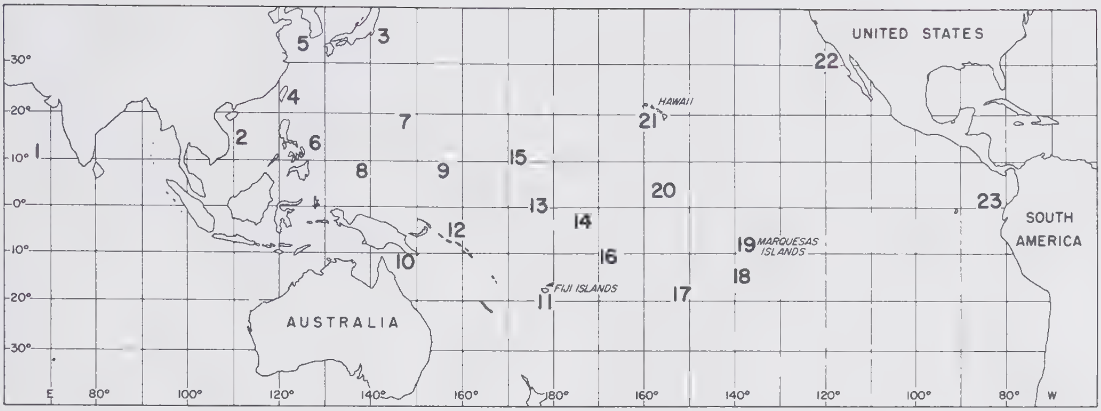

Figure 6.—Areas of baitfish availability. Numbers refer to Table 2.

erating high fishing mortality; however, better information is needed before it will be possible to manage these resources. For much of the Pacific, however, supplies of natural baits are less than required for maximum tuna production.

Aquaculture

Aquaculture is a possibility for supplying baitfishes in areas where natural baits are limited or lacking. The problems here are threefold, namely rearing a baitfish that is an acceptable bait for tuna, producing it at a competitive cost and producing it in sufficient quantity to support a number of tuna boats. The provisional bait price developed above, about $15 per Hawaiian bucket ($4.50 per kg), is sufficiently high that aquaculture should be an economically acceptable solution.

Mass rearing probably presents minimal difficulties because of a fairly extensive background in the production of fish through aquaculture.

Acceptability as discussed previously covers both mortality and effectiveness. With the Hawaiian nehu, mortality typically runs 25% per day in the baitwell, suggesting that a hardier bait produced by aquaculture that suffered only a 5% mortality rate could be 20% less effective in the production of tuna and yet be acceptable. Similarly, a less effective bait that could be produced at lower cost than nehu might, from the standpoint of economics, be an acceptable substitute bait.

In selecting a species for aquaculture, consideration has to be given to those factors affecting its acceptability, that is, hardiness and effectiveness, and those factors affecting its production, for example, can spawning be controlled? Are there difficulties in production of the young? Does it grow to an unacceptable size, etc.? Work has been done with several species—tilapia (King and Wilson, 1957), threadfin shad (Iversen, 1971), commercial sharpnosed molly (Herrick, unpublished[3]). Other species considered or tested include carp, fingerling catfish, juvenile mullet and goatfish, and golden shiner. The difficulties lie in finding species that can be raised in quantity and in devising a quantitative measure of their acceptability. For screening, a method that appears practical at present, since the characteristics of a good baitfish are poorly defined, is a series of field tests whereby sufficient quantities of bait are used in sea trials to determine its relative acceptability, that is, its mortality and effectiveness.

For work in Hawaii and using nehu as a reference bait from Table 1, it would appear that 30 kg of nehu will produce a metric ton of tuna. Screening experiments should include alternate uses of nehu and the subject bait over an extended period of time. The variance of catch rates for tuna boats is high and screening tests of the proper sensitivity cannot be conducted with small amounts of bait. In order to give an indication of effectiveness 200 buckets or enough for approximately 5 days of fishing is suggested. This will provide an initial indication as to the desirability of continuing with the species or abandoning it. The difficulty in making such a judgment is pointed out in our experience with threadfin shad whereby the results obtained during 1 year with shad aboard RV *Charles H. Gilbert* and during another trial using a commercial vessel gave different answers.

The desirability of using a saltwater versus a freshwater or a euryhaline species needs consideration since production in fresh water may present fewer problems than in salt water, the methods being better developed, and there are many freshwater species that appear to possess the characteristics desirable and necessary to be good tuna bait. However,

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[3] Herrick, S. F., Jr. 1972. Economic analysis of commercial molly *(Poecilia sphenops)* baitfish aquaculture. 11 p. and attachments. Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744.

(Opposite) Kawakawa and baitfish in tank. Tank is used for studies of behavior of fishes, including tunas.

in many island areas, sufficient fresh water for mass rearing is lacking and culture would have to be conducted in salt or brackish water. Also, there would be difficulty in maintaining fresh water in the baitwells aboard the vessel.

Transport

Another approach to bait supply is the transport of quantities of bait from an area where it is plentiful into the area of the fishery. In effect this is done in both the eastern and western Pacific by larger bait boats that bait in coastal areas and then carry the bait to the fishing grounds. The next step in this process is to transport the bait aboard a bait carrier to an area in the fishing grounds where it can be sold to the fishing vessels. This approach has not been examined in detail but it appears that using a $4.50 per kg bait price this may be feasible. This figure is based on data from the Hawaii fishery where bait usage is low owing to the large, 7 kg and up, skipjack tuna constituting the bulk of the "season fish." In areas where the average weight of the skipjack tuna is less the "value" of the bait may be expected to drop. Therefore, the profitability depends upon the amount of bait that can be carried in a given volume of water, the anticipated mortality during transport and holding at the final destination, and the value of the bait determined by its effectiveness. To evaluate such operations it is necessary to look both at the economics of shipping and the fishery, and at mortality during capture, loading, transport, unloading, and holding. Experiments conducted by the Honolulu Laboratory in transporting northern anchovy from California to Hawaii suggest that mortality in shipment may be acceptable. These shipments were made using commercial fishing vessels, which took approximately 10 days to make the crossing. Commercial shipping lines can make the crossing in about 4 days. The advent of roll-on, roll-off service between the mainland and Hawaii, for example, suggests that transport of anchovy might be practical aboard these vessels. Similarly the advent of LASH (lighter aboard ship) service to French Polynesia and American Samoa suggests that it might be feasible to ship bait from California, Latin America, or Australia to these areas. See Figure 7 for a diagrammatic summary of the preceding discussion.

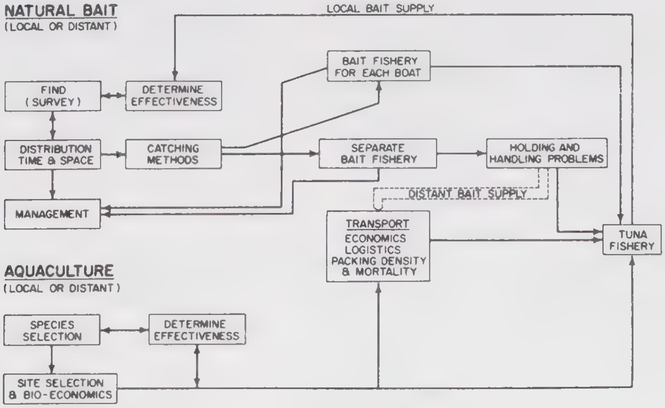

Figure 7.—Diagrammatic representation of alternative bait supply considerations.

Artificial Bait

The use of dead or inanimate substances and new live baits to replace conventional bait for surface tuna fishing should be considered. Early attempts such as those conducted at the Honolulu Laboratory in the 1950's (Tester, Yuen, and Takata, 1954) were unsuccessful, but these studies cannot be regarded as exhaustive and further experimentation should be supported. It is possible that dead baitfish or objects resembling baitfish could be made to sink and rise or move in the water so as to resemble a live baitfish. Incorporation of a scent into the objects or the use of dead bait for this purpose might serve to supplement live bait or even to replace it.

New Baits

The use of animals other than fish for bait has been suggested. Shrimp or large brine shrimp might prove to be an acceptable bait. Similarly crustacea that can be held in suspended animation or in the egg for extended periods of time might prove to be a valuable adjunct to live-bait fishing for tuna. The advantage here is that these types of animals can be produced almost upon demand and in large quantities from a small initial volume. Studies along these lines appear worthy of support although the probability of success is less likely than with aquaculture or transport.

SUMMARY

The use of live bait to catch tunas accounts for over 20% of the world tuna production. This method is especially suited for areas where tuna schools cannot be caught effectively using more efficient, that is, capital intensive, gear such as the purse seine.

Dependable supplies of acceptable

live bait are the key to successful baitfishing. Acceptable bait species are those that can be held and transported with low mortality and are effective in catching tunas, that is, the ratio of bait used to tuna caught is minimal.

Dependable supplies of natural bait do not occur in the newest tuna fishing grounds in the tropical Pacific. Ways of providing a supply include aquaculture, importation of bait from other areas, and development of artificial baits. All of these alternatives are subject to the economic constraint of an estimated $4.50 per kg value of baitfish delivered to the fishing vessel, and require varying amounts of research before they can be considered feasible. Also needed are better reporting statistics from presently used baiting grounds and the continued search for new supplies of natural bait.

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MFR PAPER 1071

Valued for meat and shells, the giant clam faces an increased harvest.

A Survey of Giant Clams, Tridacnidae, on Helen Reef, a Western Pacific Atoll

FRANK J. HESTER and EVERET C. JONES

Frank J. Hester and Everet C. Jones were formerly members of the staff of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

ABSTRACT

Transects and areal surveys by swimmers were used to estimate the standing stock of giant clams, Tridacnidae, at Helen Reef, Western Caroline Islands in March 1972. Estimates were Tridacna crocea *3.7×10^6*, T. maxima *1.7×10^6*, Hippopus hippopus *44.6×10^3*, T. derasa *32.8×10^3, and* T. gigas *49.8×10^3*. Tridacna squamosa *was not abundant or was identified as* T. maxima. *Most* T. gigas *and* T. derasa *were large, suggesting low or eratic recruitment.*

INTRODUCTION

The Indo-Pacific family Tridacnidae comprises two genera, *Tridacna* Bruguiére with five species: *Tridacna gigas* (Linné), *T. derasa* (Roding), *T. squamosa* (Lamarck), *T. maxima* (Roding), and *T. crocea* (Lamarck); and the monotypic genus *Hippopus* represented by the species, *Hippopus hippopus* (Linné). Of these six species *T. gigas* is the largest, reaching a valve length in excess of 1,300 mm and a valve weight of over 150 kg. It is this species that is the giant clam, peril to divers and an occasional bird bath or holy water font. The other species are intermediate in size with *T. crocea* being the smallest, having a maximum valve length of about 200 mm. For a description of the family and its biology and distribution see Rosewater, 1965.

All of these clams, except possibly *T. crocea*, are of value both for their meat, which is consumed locally, and for their shells, which are of value as souvenirs and to collectors. *Tridacna gigas*, *T. derasa*, and *H. Hippopus*, the larger species, are particularly sought for their shells, which currently have an ex-vessel value in Koror, Palau Islands of approximately $0.02 per millimeter for specimens over 200 mm. The shells of *T. maxima* and *T. squamosa*, being smaller, are of lesser value but they are in demand for the meats. *Tridacna crocea* is seldom utilized for any purpose.

Because of the value of the shell, as well as the potential value of the meats, and because they occur in countries that are seeking foreign exchange, the larger Tridacnidae face increased fishing pressures that may result in a major reduction of the stocks. Already the size and abundance of *T. gigas* has declined in the central Pacific, parts of the Great Barrier Reef, Indonesia, and the Philippines, probably owing to fishing pressure. In some areas the clams are now protected by law. In others, where these animals are of some importance in trade, protective measures may be necessary; however, there are very limited biological and fishery data available to suggest how stringent or what these measures should be.

John J. Naughton, a fishery biologist, with specimens of Tridacnidae.

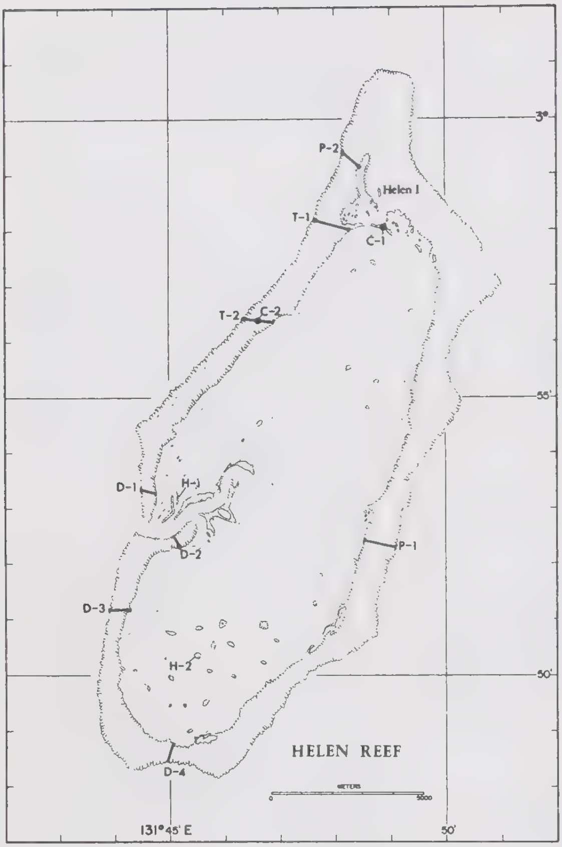


Figure 1.—Helen Reef showing location of transects.

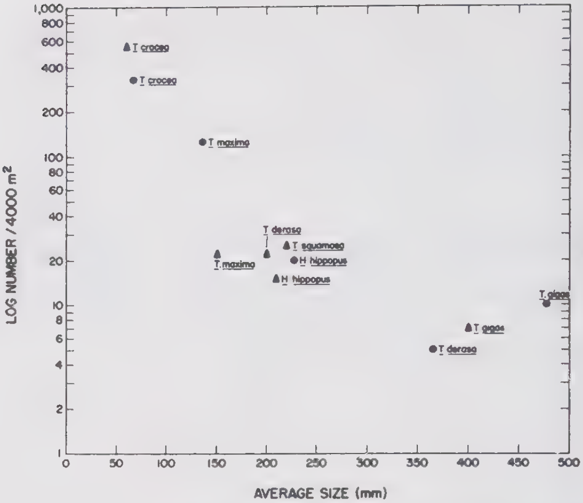


Figure 2.—Average length-frequency data of clams from Helen Reef (circles) and Palau Islands (triangles) (Hardy and Hardy, 1969).

One place that has been reasonably free from exploitation until recently is Helen Reef (Fig. 1), a small atoll to the south-southwest of the Palau Islands in the Palau District, Western Caroline Islands, of the Trust Territory of the Pacific Islands. Helen Reef lies at approximately lat.3°N, long. 131°E. It is about 24 km in its north-south dimension by 9 km in its east-west dimension and consists of reef, awash at high water, and a small sand island with coconut trees and low growth. Situated at the northern end of the reef, the island is about 1 ha (hectare) in area. The reef encloses a large lagoon with depths in excess of 60 m. The reef is about 1,200 m wide except in the north portion, which has an extended sandy area between the lagoon and the sea. A navigable passage on the western side permits access to the lagoon for vessels of moderate draft. Helen Reef lies in an area of variable winds and currents and there is no well-defined windward side although the coral growth is most luxuriant on the west side of the reef. Helen Reef is uninhabited and distant from most population centers and the reef and its associated flora and fauna are nearly untouched, being subject to only occasional visits by Trust Territory field trip ships and foreign fishing vessels. (There have been instances where the latter have been apprehended with *Tridacna* shell and turtles on board —communications from the Office of Marine Resources, Trust Territory of the Pacific Islands.)

In May 1971 and again in March 1972 the research vessel *Townsend Cromwell*, then operated by the Honolulu Laboratory of the National Marine Fisheries Service, Southwest Fisheries Center, called at Helen Reef as part of its marine resource survey of the Trust Territory of the Pacific Islands. On the latter visit of *Townsend Cromwell* a survey of Helen Reef was conducted for the Office of Marine Resources, Trust Territory of the Pacific Islands, in order to obtain a standing stock estimate of the giant clams. This had been requested because of poaching by foreign fishing boats and a growing interest on the part of the Palau District in the development of fisheries there. This report describes that survey and gives an estimate of the status of the stocks for the species found in abundance at the reef.

METHODS

Five types of surveys were used for assessing the *Tridacna* stocks: (1) Line transects: A line marked off at 100-m intervals was stretched normal to the reef from the lagoon to the seaward dropoff. The occurrence of clams within 2½ m on either side of the line was recorded, together with the

Table 1. — Helen Reef survey data.

Sta.	Type and location	Substrate notes	Distribution and abundance				Area surveyed (m²)	Density clams per 100 m²	Estimated area both sides of reef transect (ha)	Standing stock estimated numbers
T-1	Linear transect running 285° T from a pipe located at lat. 2°58′00″N, long. 131°48′16″E.	Transect ran from lagoon dropoff (5 m depth) to sea, a distance of 1,500 m. Inner 500 m sand and coral heads (water depth 1.5-2 m) turning to sand; coral and coral rubble 500-1,100 m algal flat and hard reef from 1,100 m to dropoff. The outer 7-800 m is exposed to low water.	*Inner 500 m*	*Mid-500 m*	*Outer 500 m*	*Total*				
			2 *T. gigas*		1 *T. gigas*	3	7,500	0.04	520	2,080
			5 T. derasa	2 T. derasa	1 *T. derasa*	8		0.107		5,500
				2 *H. hippopus*	5 *H. hippopus*	7		0.093		4,853
			T. crocea and *T. maxima* ubiquitous							
T-2	Linear transect running 277° T from a pipe located at lat. 2°56′20″N, long. 131°46′53″E.	Essentially the same as T-1 except transect ended at wrecked freighter 1,100 m from Lagoon across reef. From 300 to 800 m the reef was carpeted with living coral (*Acropora* sp.).	*Inner 300 m*	*Mid-300 m*	*Outer 300 m*	*Total*				
				11 *T. gigas*	5 *T. gigas*	16	5,500	0.29	800	23,273
			2 *T. derasa*	25 *T. Derasa*	6 *T. derasa*	33		0.60		48,000
				1 *H. hippopus*	7 *H. hippopus*	8		0.145		11,636
					1 *T. squamosa*	1				
			T. crocea and *T. maximus* ubiquitous							
C-1	Areal survey of circle 25 m radius around a pipe located at lat. 2°58′03″N, long. 131° 48′56″E.	On shallow finger (2 m depth) of reef extending into lagoon. Massive *Porites* sp. and sand and rubble.	*T. gigas*			4	2,000	0.20	520	10,400
			T. derasa			3		0.15		7,800
			H. hippopus			3		0.15		7,800
			T. maxima			62		3.10		
			T. crocea			200		10.0		
C-2	Areal survey of circle 25 m m radius around a pipe located at lat. 2°56′18″N, long. 131°46′36″E.	On coral carpet midway through T-2.	*T. gigas*			6	2,000	0.30	800	24,000
			T. derasa			2		0.10		8,000
			H. hippopus			13		0.65		52,000
			T. maxima			63		3.15		
			T. crocea			138		6.90		
D-1	Drift transect starting from lat. 2°53′15″N, long. 131°44′45″E. Course 282° T.	Transect ran 600 m across reef of mostly hard coral flat and large rubble.	*T. gigas*			3	3,000	0.10	175	1,750
			T. derasa			4		0.13		2,333
			H. hippopus			6		0.20		3,500
D-2	Drift transect starting from lat. 2°52′18″N, long. 131°45′14″E. Course 330°T.	Transect ran 440 m across sand and coral heads.	No large clams seen				2,200		140	
D-3	Drift transect starting from lat. 2°51′10″N, long. 131°44′16″E. Course 266° T.	Transect ran 700 m from sand and large coral heads to reef flat and rubble. Large *T. gigas* and *T. derasa* along lagoon in 2-3 m water. Power tows made between D-3 and D-4.	*T. gigas*			3	3,500	0.086	430	3,686
			T. derasa			3		0.086		3,686
			H. hippopus			4		0.114		4,914
D-4	Drift transect starting from lat. 2° 48′ 46″ N, long. 131° 45′ 06″ E. Course 200° T.	Transect ran through dirty water 820 m across sand and mostly dead coral. Large clams along lagoon and first 200 m of transect. Power tows made between D-4 and P-1.	*T. gigas*			2	4,100	0.049	550	2,683
			T. derasa			3		0.073		4,024
			H. hippopus			5		0.122		6,707
P-1	Transect under power from lat. 2°52′25″N, long. 131°48′30″E. Course 100° T.	Transect ran 1,200 m. Clams along lagoon in *Acropora* sp. rubble, some signs of *Acanthaster* at work. Few clams on reef except for sandy areas seen on power tows made between P-1 and P-2.	*T. gigas*			3	6,000	0.050	1,950	9,750
			T. derasa			2		0.033		6,470
			H. hippopus			4		0.066		13,000
P-2	Transect under power from lat. 2°59′05″N, long. 131°48′30″E. Course 311° T.	Transect ran 1,100 m across sand and scattered coral heads, 1-1.5 m depth. Only large *T. gigas* and *T. derasa*.	*T. gigas*			6	5,500	0.109	600	6,545
			T. derasa			7		0.127		7,636
H-1	Coral head at lat. 2°53′13″N, long. 131°45′14″E.	Lovely live coral, many clams, small and medium, 1-4 m depth.	*T. gigas*			13	900	1.44	175	25,270
			T. derasa			17		1.89		33,075
			H. hippopus			2		0.22		3,888
H-2	Coral head at lat. 2°50′24″N, long. 131°45′30″E.	Fine flat head, small and medium clams, live coral 2-3 m depth.	*T. gigas*			23	1,600	1.44	175	25,270
			T. derasa			19		1.19		20,781
			H. hippopus			6		0.38		6,562
				TOTAL	*T. gigas*	82	43,800 m²		6,835 ha	
					T. derasa	101				
					H. hippopus	58				

Table 2.—Abundance of clams at Helen Reef and the Palau Islands. Numbers adjusted to 2,000 m².

Species	Circle No. 1	Circle No. 2	Transect No. 1	Transect No. 2	Hardy & Hardy
T. crocea	138	200	Not counted		275
T. maxima	63	62	Not counted		11
H. hippopus	13	4	3	3	8
T. squamosa	0	0	0	1	13
T. derasa	2	3	3	15	11
T. gigas	6	4	1	10	4

general bottom type and the water depth. Only the three largest species, *T. gigas*, *T. derasa*, and *H. hippopus*, were recorded, and *T. gigas* and some *T. derasa* were measured. (2) Areal: Two circles, each with a radius of 25 m (2,000 m²), were laid out around reference stakes. All of the clams occurring within this circle were counted and measured. (3) Drift transects: A small boat was allowed to drift across the reef with the current while swimmers holding on to the side counted *H. hippopus* and *T. derasa* and counted and measured *T. gigas* and some *T. derasa*. (4) Towing: The boat under power towed swimmers slowly across the reef, and they counted the three largest species. (5) Power tows: Swimmers were towed along the reef between transects to estimate the densities of clams. Power towing provided an indication of the variability of the occurrence of clams in areas of the reef between transects.

The centers of the two circular surveys and the starting points of the two line transects were marked with bronze pipes imbedded in quick-hardening cement. The locations of these marks to the nearest second of arc are given in Table 1, together with the starting points and directions of the drift and tow transects. All positions are taken from the Navy Hydrographic Office chart of Helen Reef, No. 6072, 1st edition, April 1944. Areas not actually measured by transect were taken from the chart with a planimeter. All clam measurements are straight-line valve length made with meter stick calipers, a method that was unsatisfactory for the larger specimens owing to the shortness of the caliper jaws and the width (curvature) of the valves. The estimated error of measurement was ± 5 mm for clams up to 400-mm shell length. For clams larger than this, the error was probably on the order of ± 25 mm.

RESULTS

The abundance of clams at Helen Reef for the two transects and the two circle surveys is presented in Table 2 with abundance data from the Palau Islands (Hardy and Hardy, 1969) for comparison. For this table both our data and Hardy and Hardy's data have been adjusted to number of clams per 2,000 m² (the area of each circle survey).

Average shell size and log abundance adjusted to 4,000 m² (equivalent to the two circle surveys combined) for the six species are given in Figure 2. Average sizes for Hardy and Hardy's clams were estimated from their Figure 4 and are subject to interpretive error.

Length-frequency data for all *T. gigas* and *T. derasa* measured and for *T. crocea*, *T. maxima*, and *H. hippopus* from the two circle surveys combined are presented in Figure 3.

Measured by planimeter, the area of Helen Reef judged suitable habitat for clams is approximately 5,340 ha. Standing stock estimates for the three larger species were made in several ways. From the data in Table 1 the total numbers counted and the total area surveyed were converted to density per hectare which, when multiplied by total reef area, gave estimates of standing stock. Second, densities calculated for each transect were extrapolated to standing stock for adjacent sections of the reef to adjust for habitat variability. Because the data were available from both linear and areal surveys in two sections, estimates were made using each set independently. Third, estimates based on the two coral heads surveyed resulted in surprisingly high

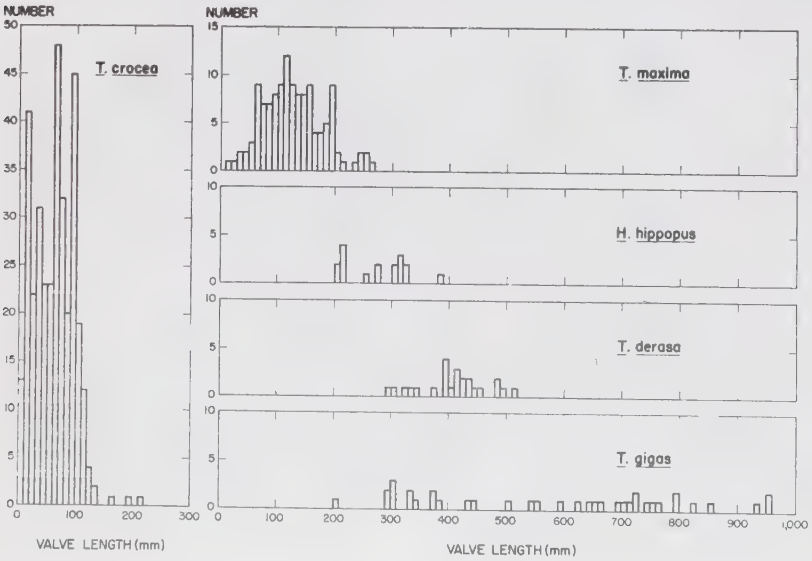


Figure 3.—Length frequency of Tridacnidae at Helen Reef.

standing stock estimates, so total standing stock was calculated with and without the coral head data. Fourth, for the two smaller species, *T. maxima* and *T. crocea*, estimates were made by extrapolating the areal survey data to total reef area resulting in a probable overestimate of abundance. From these estimates maximum and minimum standing stock are obtained (Table 3).

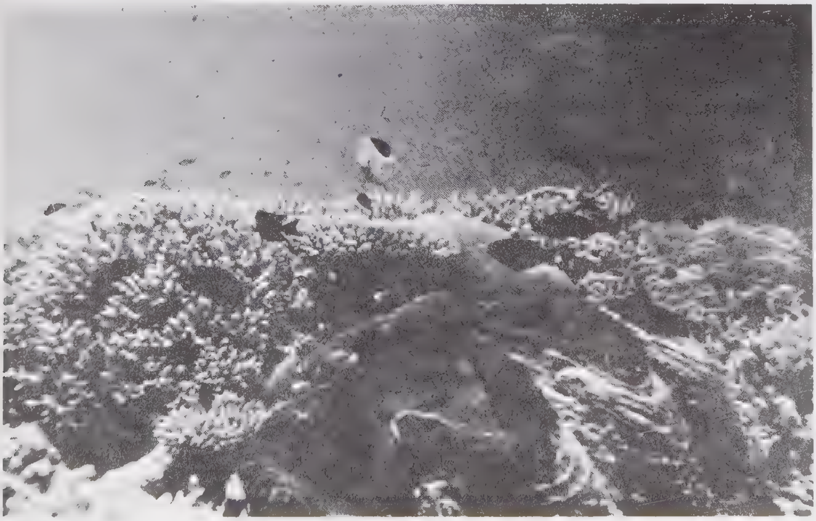
DISCUSSION

Tridacna squamosa was exceedingly rare at Helen Reef, only one specimen being found, whereas *T. maxima* was abundant. This differed from the pattern in the Palaus (Hardy and Hardy, 1969).

The smallest *T. gigas* found was a 200-mm specimen and only two specimens of *T. gigas* shorter than 300 mm were observed. We thought it might be possible to make some recruitment and growth rate estimates by looking for modal size groups with *T. gigas*. However, our measurements are too few to permit any inferences to be drawn.

The growth rates of giant clams are subject to debate in the literature, estimates ranging from a few millimeters per year to an excess of 50 mm per year (see Rosewater, 1965). Observations from Eniwetok based on radioautographs (Bonham, 1965) together with our observations that encrusting coral on the shells seldom is very large, suggest that the growth rates are relatively rapid and that large *T. gigas* probably are 10-20 years of age. Hardy and Hardy's data suggest that the Palaus' *T. gigas* and *T. derasa* are smaller on the average than our Helen Reef clams. For *T. gigas* this may be the result of our extrapolation and interpretation of their data, but in the case of *T. derasa* a size difference appears likely.

With regard to distribution our observations were very similar to Hardy and Hardy's and the rest of the literature. *Tridacna crocea* usually was imbedded in coral heads (*Porites* sp.). *Hippopus hippopus* was found on sandy areas and on occasion on the reef flat, and *T. maxima* was attached to suitable substrate out into the surf zone. *Tridacna derasa* and *T. gigas* occurred in various habitats. To the north of Helen Island, there is an extensive sand flat with occasional small coral patches. Here we found large *T. derasa* and *T. gigas*. Large



The giant clam, shown top and lower left in its natural habitat, is hoisted aboard ship, lower right.

Table 3. — Standing stock estimate.

	Based on number per ha			Based on number per survey sector	
Species	Density no ha	Standing stock		T−1 + T−2	C−1 + C−2
T. gigas	18.72	99.97×10^3		49.77×10^3	58.81×10^3
T. derasa	26.94	143.86×10^3		77.65×10^3	32.75×10^3
H. hippopus	13.47	71.90×10^3		44.61×10^3	87.92×10^3
T. maxima	3.10×10^2	1.66×10^6			
T. crocea[1]	10.00×10^2	5.34×10^6			
				Plus H-1	Plus H-1
T. maxima	3.15×10^2	1.68×10^6	*T. gigas*	75.04×10^3	83.08×10^3
T. crocea[2]	6.90×10^2	3.68×10^6	*T. derasa*	110.73×10^3	65.83×10^3
			H. hippopus	48.49×10^3	91.80×10^3
	High estimate	Low estimate			
T. gigas	99.97×10^3	49.77×10^3			
T. derasa	143.86×10^3	32.75×10^3			
H. hippopus	94.48×10^3	44.61×10^3			
				Plus H-2	Plus H-2
T. maxima	1.68×10^6	1.66×10^6	*T. gigas*	75.04×10^3	83.06×10^3
T. crocea	5.34×10^6	3.68×10^6	*T. derasa*	97.93×10^3	58.53×10^3
			H. hippopus	$51 17 \times 10^3$	94.48×10^3

[1] Estimates for *T. maxima* and *T. crocea* from survey C-1.
[2] Estimates for *T. maxima* and *T. crocea* from survey C-2.

T. gigas also occurred along the lagoon edge of the reef south of the pass. Small, medium, and large *T. gigas* and *T. derasa* were found on the coral heads in the lagoon and associated with *Acropora* sp. rubble along the east side of the lagoon. The east and south flats of the reef were hard and relatively bare compared with the west and north sections of the reef except for some sandy portions where *T. gigas* and *T. derasa* were found.

CONCLUSIONS

The clam populations at Helen Reef appeared to be large at the time of the survey. The lack of small *T. gigas* and *T. derasa* suggests that recruitment may be erratic or slow or both. Our lowest standing stock estimates of these two species, the most desirable for shell, are 49.8×10^3 *T. gigas* and 32.8×10^3 *T. derasa*, suggesting that a moderate fishery for these two species could be prosecuted. Uncertainties with regard to growth rates and recruitment advise caution.

SUMMARY

A standing stock estimate of giant clams, Tridacnidae, at Helen Reef, a small coral atoll in the western Pacific (lat.3°N, long.131°E), was made in March 1972. Eight transects of the reef were made together with two areal surveys 2,000 m^2 each. From these transects, high and low estimates of standing stock for five species of clams, *T. gigas*, *T. derasa*, *T. maxima*, *T. crocea*, and *H. hippopus* were made. Low estimates for the stocks were: *T. gigas* 49.8×10^3, *T. derasa* 32.8×10^3, *T. maxima* 1.7×10^6, *T. crocea* 3.7×10^6, and *H. hippopus* 44.6×10^3. Only one specimen of the sixth clam, *T. squamosa*, was encountered.

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FEEDING RELATIONSHIPS OF TELEOSTEAN FISHES ON CORAL REEFS IN KONA, HAWAII

Edmund S. Hobson[1]

ABSTRACT

Feeding relationships of teleostean fishes on coral reefs at Kona, Hawaii, were studied during 1969 and 1970.

Fishes that have a generalized feeding mechanism, including those carnivores whose morphologies place them close to the main line of teleostean evolution, are predominantly nocturnal or crepuscular. These include holocentrids, scorpaenids, serranids, apogonids, priacanthids, and lutjanids. The major prey of the nocturnal species are small, motile crustaceans, which are most available to the direct attacks of generalized predators when they leave their shelters after dark. The major prey of the crepuscular species are smaller fishes, whose defenses against direct attacks of generalized predators are less effective during twilight. Feeding by generalized predators during the day depends largely on being within striking distance of prey that make a defensive mistake, a position best attained by those predators that ambush their prey from a concealed position, or by those that stalk.

Ambushing and stalking tactics have produced some highly specialized forms that, during the day, prey mostly on smaller fishes. Diurnal ambushers include the highly cryptic synodontids, scorpaenids, and bothids; diurnal stalkers include aulostomids, fistulariids, belonids, and sphyraenids—all of them long, attenuated fishes.

Some predators—most notably the muraenid eels—are specialized to hunt deep in reef crevices, and here they capture some of the many small animals that shelter themselves in those crevices, day and night, when resting, injured, or distressed. Mullids use their sensory barbels to detect small animals that have sheltered themselves amid the superficial covering on the reef, or in the surrounding sand; at least some mullids further use their barbels to drive these prey into the open.

Most of the fishes on Kona reefs are among the more highly evolved teleosts, having reached, or passed, the percoid level of structural development. The adaptability of the feeding apparatus in these more advanced groups has given rise to a wide variety of specialized species, including both carnivores and herbivores, that have diverged from one another mostly on the basis of differing food habits. These fishes, most of which are diurnal, include the chaetodontids, pomacentrids, labrids, scarids, blenniids, acanthurids, and *Zanclus,* among the perciforms; and the balistids, monacanthids, ostraciontids, tetraodontids, canthigasterids, and the nocturnal diodontids, among the tetraodontiforms. With their specialized feeding structures and techniques, these fishes consume organisms like sponges, coelenterates, large mollusks, tunicates, and tiny or cryptic crustacea that are protected by behavioral or anatomical features from fishes not appropriately specialized.

Many important ecological relations among marine fishes are understood only by considering in broad overview during both day and night the different forms living together under natural conditions. With this in mind, I undertook a broad study of reef fishes at Kona, Hawaii, between June 1969 and August 1970. A segment of this study dealing with the twilight situation was published earlier (Hobson, 1972). The present report describes the situations that prevail throughout day and night. The work is centered on direct observations of activity in the fishes, as was my earlier study of predatory behavior of shore fishes in the Gulf of California (Hobson, 1968a), but here with greater emphasis on detailed analysis of food habits.

Several other workers adopted broad overviews in considering fishes of various areas. Limbaugh (1955) studied fishes in California kelp beds during the day, whereas Starck and Davis (1966) described the habits of fishes in the Florida Keys at night; both of these studies present extensive direct observations of activity, but little data on food habits. On the other hand, Hiatt and Strasburg (1960), as well as Randall (1967), and Quast (1968), treated extensively the food habits of fishes collected during daylight in the Marshall Islands, the West Indies, and southern California, respectively, but offered relatively few direct observations of activity. Suyehiro (1942) comprehensively treated the feeding morphology of fishes in Japan

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and included data on food habits; however, he included little information on activity. The 1970 United States Tektite II program provided many scientists with the opportunity to make direct observations on a Virgin Island reef, and reports concerning the fishes have been published in one volume (Collette and Earle, 1972). Many other reports of limited scope are scattered through the literature, most of them being fragmented data on food habits; nevertheless, accounts of activity based on direct observations are sparse, especially of nocturnal activity.

The great variety of feeding mechanisms for which teleostean fishes are so well known occur among coral-reef fishes far more so than among the fishes of any other habitat. I take advantage of this circumstance in the discussion that concludes the present report and consider the feeding relationships among fishes on Kona reefs in the context of teleostean evolution.

METHODS

Direct Observations

I observed activity of the fishes during 632 h underwater at all periods of day and night using scuba and by snorkeling. Except when collecting specimens, I tried not to influence the fishes or their environment, hoping that events were taking a natural course. Fishes considered in this report are those that can be seen by an underwater observer at some time during day or night. Although this includes by far most of the reef fishes, some abundant species are not included because they remain secreted in the reef at all hours.

Food Habits

The gut contents of 1,547 fish specimens of 102 species were analyzed. With a few isolated exceptions, noted below, all the specimens were collected with spears. I find spearing the most effective way to collect fishes for study of food habits. Using this method, specimens were collected in specific locations at the times of day and night that best define diurnal-nocturnal activity patterns. Because I speared all the specimens myself, I know what each individual was doing when captured, and this knowledge significantly influenced analysis of the data. Even the response of the various fishes to being stalked and speared (or missed) provided certain behavioral insights.

Food habits change over the life of at least most fishes, usually along with recognizable changes in behavior and morphology. Unless otherwise indicated, specimens selected for this study showed behavior and morphology judged typical of adults.

The collections were spread over time and space, so that possible effects of transient localized, perhaps atypical, situations were reduced. Generally, only a single individual of any one species was collected during a single period of observations; thus, for a given species, most individuals each represent a separate collecting station. For these reasons, I judge the data from the food habit analysis to accurately represent the situation existing on Kona reefs over the 15 mo of this study.

The collections were spaced throughout day and night, so that relative digestion of gut contents supplements direct observations of activity in determining specific feeding times. All specimens were sealed in individual plastic bags immediately after being speared, most while still underwater. Gut contents of specimens collected while snorkeling were preserved immediately by injecting a concentrated formaldehyde solution directly into the gut cavity, whereas gut contents of fishes taken by scuba were preserved as soon as possible after emerging from the water. I was unable to see a difference in the digestion undergone by material collected in each of these two ways, suggesting that digestion is sharply curtailed by the death of the fish. Where practical, identifications of items in the guts were carried far enough to establish such general prey characteristics as habitat and mode of life.

Quantifying Food Habits

For those species represented by enough numbers in the analysis of gut contents, I state: 1) the number of fish of that species containing each food item, and 2) the mean percent of that item in the *diet volume,* which is the total volume of gut contents in all specimens of that species. This second figure was calculated from estimates of the percent each item taken by the species contributed to the gut contents of each individual fish (0 to 100%). The food items are listed in order of a *ranking index,* which is computed by multiplying the ratio of fish containing the item to the number of fish sampled, by the mean percent that item represented of the diet volume. Thus, for example, for *Holocentrus sammara* (Table 10), the number one prey, xanthid crabs, has a ranking index of

$12/17 \times 52.5 = 37.05$. The data are tabulated when there are more than a few items in the gut contents of a given species.

In species with a well-defined stomach, usually only stomach contents were analyzed, as materials in the intestines generally were too far digested for satisfactory analysis. On the other hand, some fishes that do not have a well-defined stomach have much material in their intestine that is suitable for study, and so was included in the analysis. Thus data sometimes are specified as being from stomach contents, but at other times the more general term gut contents is used.

Transect Counts

To characterize the fishes inhabiting each of the various inshore habitats described below, 100-m transect lines were established in locations judged typical of each habitat. Twenty-two counts of fishes within 5 m of transect lines at 17 sites representing five habitat categories (see below) were made between September 1969 and May 1970; at least 1 mo passed between counts in any one habitat.

Quantifying Relative Abundance

In the Tables below that present data from the transect counts, the relative abundance of the different species is represented by a relative abundance index. This is the percentage that species represented of all fishes (individuals) counted along all transect lines in that habitat.

Assessing Nocturnal Colorations

A number of species possess distinctive day and night differences in coloration. Earlier (Hobson, 1968b), I discussed the problem of distinguishing true nocturnal hues from those elicited as a response to the diving light—a frequent source of error in literature reports of nocturnal color patterns. No color pattern that becomes intensified under the diving light is considered here to be a nocturnal pattern; the vast majority described herein were in fact almost immediately lost when the fish was illuminated.

Study Area

The study area extends 7.7 km along the southwestern shore of the Island of Hawaii, from Keawekaheka Point just north of Kealakekua Bay, to Alahaka Bay, south of Honaunau (Figure 1). This is part of what is known as the Kona coast. Except for short stretches of sand and cobble beaches at Napoopoo and Keei, the shoreline is a rough basalt face that drops abruptly into the sea from 2 to 3 m above the water's surface (Figure 2), to a similar depth below. From the base of this face the sea floor slopes down to water depths of about 20 to 30 m, about 50 to 600 m from shore, then falls away sharply to much greater depths. Thus, along this coast water less than 20 m deep is limited to a relatively narrow shelf, the outer rim of which provided a convenient natural boundary to the study area (Figure 1).

Environmental conditions in Kona are remarkably constant, which greatly aided this study. Surface water temperatures ranged from 29°C in the fall to 22°C in the spring, but I noted no marked seasonal variations among the fishes either in their activity or species composition. Conditions

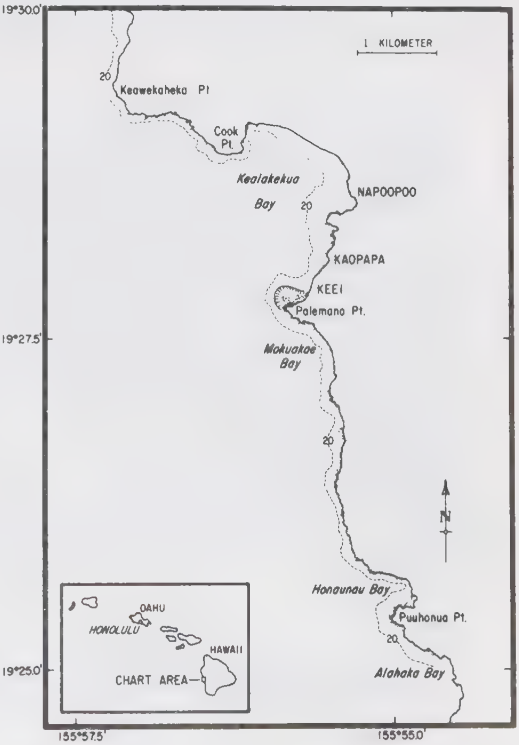

FIGURE 1.—The study area along the Kona coast, Island of Hawaii. Adapted from C. & G.S. chart 4123. Depth contour in meters.

are especially moderate on the Kona coast, in part because towering volcanoes shelter the area from the trade winds.

THE INSHORE HABITATS AND THEIR CHARACTERISTIC FISHES

The study area in Kona encompasses a variety of submarine habitats, each with a distinctive assemblage of fishes. For convenience, these habitats are here grouped subjectively into five categories: 1) coral-rich habitat, 2) boulder habitat, 3) shallow reef-flat habitat, 4) reef-face habitat, and 5) outer drop-off habitat. Along with the following habitat descriptions, there are listed the 10 fish species most often seen in each habitat, as observed in the transect counts.

Coral-Rich Habitat

In many places where there is shelter from the long Pacific swells, the sea floor in water between 2 and 12 m deep is richly overgrown with corals (Figure 3). The predominant coral is *Porites pukoensis,* which grows in a variety of massive formations. Examples occur in Honaunau Bay, in the lee of Palemano Point, and in the sheltered waters on the north side of Kealakekua Bay (Figure 1). Overall in the parts of the study area that are richly overgrown with corals, *P. pukoensis* variably shares dominance with another form, *P. compressus,* that grows as fingerlike branches 10 to 20 mm in diameter. *Porites compressus* is dominant where there is increased exposure to the prevailing swell, but where there is still some protection from a lee shore or increased water depth. Thus, in the middle of both Kealakekua Bay and Honaunau Bay, as well as in much of the study area where the water is more than about 15 m deep, broad fields of fingerlike *P. compressus* dominate the scene. In extreme situations, habitats dominated by either one of these coral forms are as distinct from one another in their characteristic faunas as any two habitat types characterized here. I group the two coral habitats together because in most of the coral-rich areas where observations were made during this study

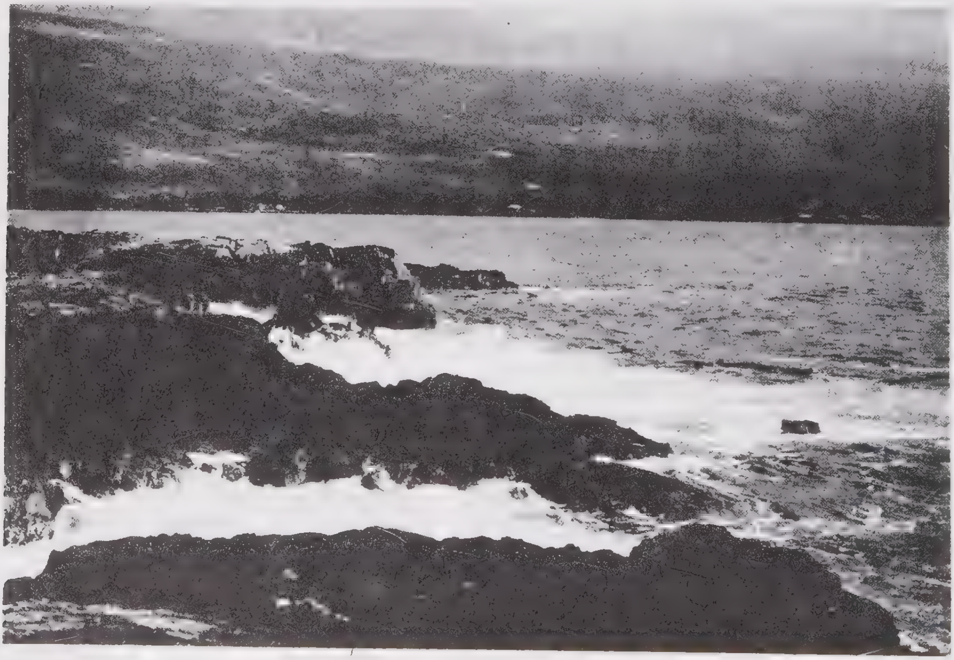

FIGURE 2.—The shoreline at Cook Point, Kealakekua Bay (looking southeast), which is typical of the shoreline throughout most of the study area.

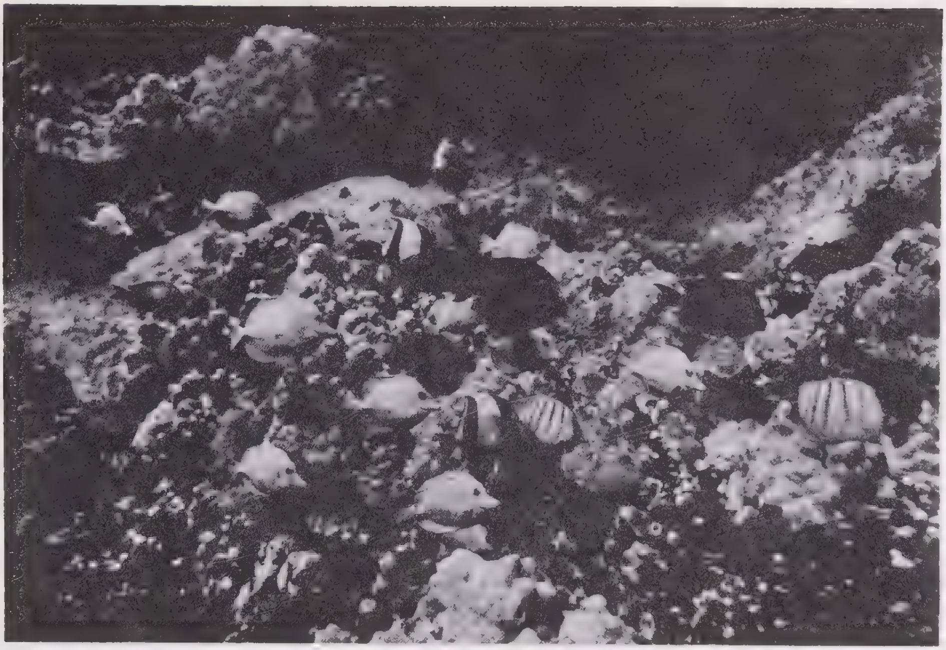

FIGURE 3.—Coral-rich habitat. Fishes shown include: *Chaetodon multicinctus, Ctenochaetus strigosus, Zebrasoma flavescens, Acanthurus nigrofuscus,* and *Zanclus canescens.*

the two forms of *Porites* share dominance. Nevertheless, the fishes listed in Table 1,[2] which are characteristic of those seen in the coral-rich habitat by day, were observed where *P. pukoensis* was the more dominant coral. Table 2[3] lists fishes characteristic of those seen in this same habitat at night. Because of difficulties inherent in making transect counts after dark, data in Table 2 are only rough approximations; they are presented primarily to illustrate the differing situation after dark, and to emphasize that the other counts reflect a situation characteristic of daytime only.

Boulder Habitat

From shore to depths of about 15 m throughout that part of the study area lying off exposed shorelines, the sea floor is strewn with basalt boulders. Often these boulders are dotted with various algae and corals—mostly encrusting varieties—but because these forms are small, the

TABLE 1.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 5$
1	*Ctenochaetus strigosus*	15.45	5
2	*Chromis leucurus*[1]	12.30	5
3	*Zebrasoma flavescens*	10.58	5
4	*Pomaentrus jenkinsi*	6.71	5
5	*Thalassoma duperrey*	5.71	5
6	*Chaetodon multicinctus*	4.41	5
7	*Acanthurus nigrofuscus*	4.37	5
8	*Acanthurus nigroris*	3.64	3
9	*Plectroglyphidodon johnstonianus*	3.07	5
10	*Centropyge potteri*	2.49	2

[1] In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report)

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[2] Table 1 is based on data from five transects at four coral-rich sites—two at Honaunau, and two at Kaopapa in Kealakekua Bay (see Figure 1). Total number of species observed on these five transects: 82; mean number of individuals of all species for a single transect: 522.

[3] Table 2 is based on data from three nocturnal transects (one on a dark night, two on moonlit nights) at three coral-rich sites—two at Honaunau, one at Kaopapa in Kealakekua Bay (see Figure 1), all three of which were also used in daytime counts (Table 1). Counts were made by switching on a light briefly about every 10 m as we swam along the line. Listing of a species does not necessarily imply activity; as becomes clear in the species accounts, below, some of these fishes are inactive on or near the reef at night. Total number of species observed on these three transects: 36; mean number of individuals of all species for a single transect: 165.

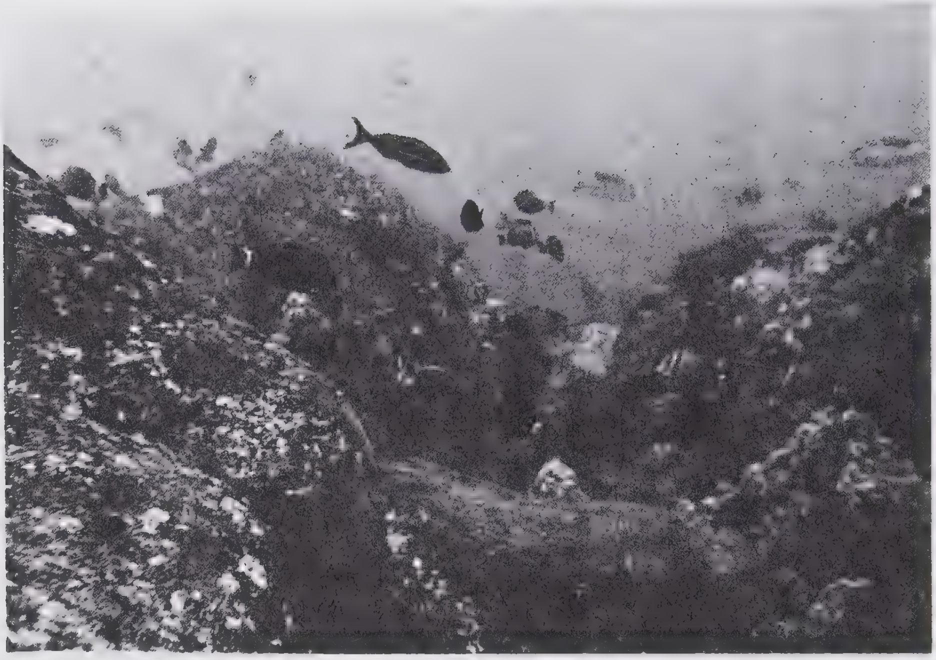

FIGURE 4.—Boulder habitat. Fishes shown include: *Aphareus furcatus, Monotaxis grandoculis* (showing barred color pattern), *Acanthurus leucopareius,* and *Zebrasoma flavescens.*

TABLE 2.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat at night.

Rank	Species	Relative abundance index	No. times in top 5 of individual transects $n = 3$
1	*Myripristis kuntee*	23.61	3
2	*Apogon menesemus*	14.52	3
3	*Myripristis murdjan*	12.33	2
4	*Apogon snyderi*	11.90	3
5	*Zebrasoma flavescens*	6.85	2
6	*Chaetodon multicinctus*	4.03	0
7	*Acanthurus sandvicensis*	2.40	1
8	*Acanthurus nigroris*	2.22	0
9	*Holocentrus lacteoguttatus*	1.21	0
10	*Chaetodon ornatissimus*	1.21	0

TABLE 3.—The 10 fish species most frequently seen along transect lines in the boulder habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Acanthurus nigrofuscus*	13.74	4
2	*Ctenochaetus strigosus*	10.77	4
3	*Zebrasoma flavescens*	9.61	4
4	*Acanthurus achilles*	8.00	4
5	*Thalassoma duperrey*	6.44	4
6	*Pomacentrus jenkinsi*	5.25	4
7	*Acanthurus nigroris*	4.88	3
8	*Acanthurus leucopareius*	4.73	4
9	*Abudefduf sindonis*	3.64	4
10	*Chromis vanderbilti*	2.35	3

general appearance is one of bare rocks (Figure 4). Especially in the shallower regions, but decreasing with greater depths, this habitat is regularly swept by a strong surge. At depths varying with the relative proximity of a lee shore or protecting reef, but usually at about 12 to 17 m, the boulder habitat in many locations grades into the fields of fingerlike *Porites compressus,* one of the coral-rich habitats described above. Fishes listed in Table 3 [4] are characteristic of those seen in the boulder habitat during the day.

Shallow Reef-Flat Habitat

Shallow surge-swept reefs, the remains of ancient lava flows, extend offshore in several locations (Figure 5). Here, a solid pavement of exposed basalt, containing many cracks and crevices, supports a distinctive array of marine organisms. The predominant benthic life form is the coral

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[4] Table 3 is based on data from four transects at four boulder sites—one at Cook Point, one at Mokuakae Bay, and two at Alahaka Bay (see Figure 1). Total number of species observed on these four transects: 77; mean number of individuals of all species for a single transect: 672.

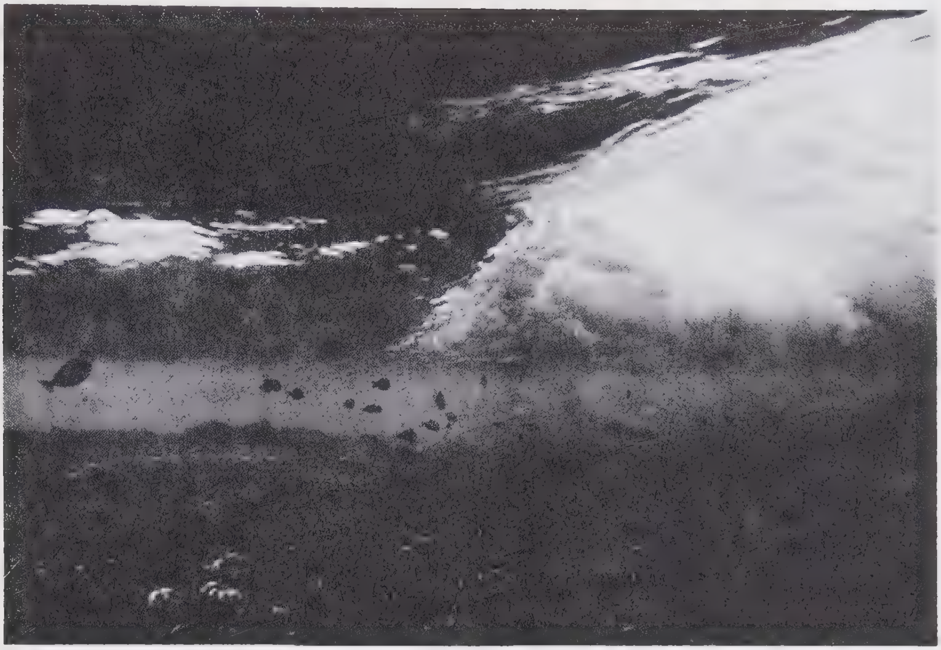

FIGURE 5.—Shallow reef-flat habitat. Most of the fishes shown are acanthurids, and include *Naso lituratus* and *N. unicornis*.

Pocillopora meandrina, growing as isolated heads 10 to 50 cm wide. The outstanding characteristics of this habitat, which generally has a maximum water depth of only about 3 to 4 m, are extreme water movement and wave shock. The fishes listed in Table 4 [5] are characteristic of those seen on shallow reef flats during the day.

TABLE 4.—The 10 fish species most frequently seen along transect lines in the shallow reef-flat habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Acanthurus nigrofuscus*	20.23	3
2	*Thalassoma duperrey*	17.41	3
3	*Abudefduf imparipennis*	15.12	3
4	*Chromis vanderbilti*	10.33	3
5	*Thalassoma fuscus*	4.78	3
6	*Stethojulis balteata*	2.88	3
7	*Gomphosus varius*	2.78	3
8	*Naso literatus*	2.02	1
9	*Zebrasoma flavescens*	1.79	1
10	*Pomacentrus jenkinsi*	1.67	1

Reef-Face Habitat

At the offshore edge of the shallow reef flats, and at many locations along the shore, a sheer basalt face falls precipitously to water depths of 10 to 15 m (Figure 6). This situation produces a wide range of conditions within a limited area. In its upper regions the surge and wave shock are that of the reef-top habitat, but these rapidly abate with increasing depth. Conditions adjacent to the base of the reef face are essentially those of the boulder habitat, with fragmented pieces of the reef lying about as large boulders. The predominant forms of benthic life, dotting the rock surfaces, are *Pocillopora meandrina* (in the shallower regions), and smaller encrusting corals and algae. Many planktivorous fishes are concentrated in the water column adjacent to the reef face. Understandably, there is a greater variety of fishes in this habitat than in the other habitats characterized here. Fishes listed in Table 5 [6] are characteristic of those seen along the reef face during the day.

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[5] Table 4 is based on data from three transects at three shallow reef-flat sites at Palemano Point (see Figure 1). Note: one of the transect counts was aborted after 60 m when the surge became too strong to continue. Total number of species observed on these three transects: 54; mean number of individuals of all species for a single transect: 578.

[6] Table 5 is based on data from three transects at two reef-face sites at Palemano Point (see Figure 1). Total number of species observed on these three transects: 89; mean number of individuals of all species for a single transect: 937.

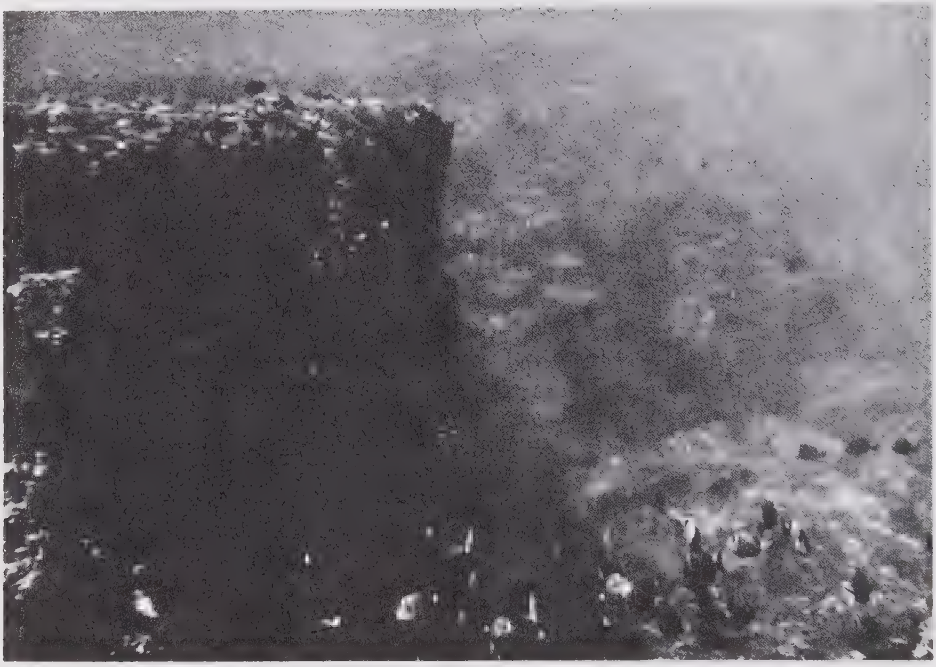

FIGURE 6.—Reef-face habitat. Most of the fishes shown swimming at the base of the reef are *Acanthurus leucopareius*. The reef face shown here drops 8 to 10 m.

TABLE 5.—The 10 fish species most frequently seen along transect lines in the reef-face habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Chromis vanderbilti*	11.74	3
2	*Ctenochaetus strigosus*	9.54	3
3	*Zebrasoma flavescens*	9.11	3
4	*Acanthurus leucopareius*	7.18	3
5	*Acanthurus nigrofuscus*	6.17	3
6	*Thalassoma duperrey*	4.41	3
7	*Pomacentrus jenkinsi*	3.95	3
8	*Abudefduf abdominalis*	3.56	3
9	*Acanthurus achilles*	3.56	3
10	*Melichthys niger*	3.38	3

Outer Drop-Off Habitat

At the rim of the outer drop-off, 50 to 600 m from shore, where the sea floor falls abruptly from about 25 m to much greater depths, the sea floor generally is overgrown with the fingerlike form of *Porites compressus,* interspersed with massive heads of *P. pukoensis,* bare basalt boulders, and sand patches (Figure 7). The most striking characteristic of this habitat, aside from the spectacular way the sea floor falls away, is the large number of planktivorous fishes that abound in the water column. Obviously conditions for feeding on plankton are especially well developed here. The fishes listed in Table 6 [7] are characteristic of those seen on the rim of the outer drop-off during the day.

TABLE 6.—The 10 fish species most frequently seen along transect lines in the outer drop-off habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Naso hexacanthus*	11.39	4
2	*Chromis leucurus*[1]	11.19	4
3	*Xanthichthys ringens*	10.50	4
4	*Thalassoma duperrey*	6.64	4
5	*Zebrasoma flavescens*	4.76	3
6	*Ctenochaetus strigosus*	3.87	2
7	*Chaetodon multicinctus*	3.76	3
8	*Centropyge potteri*	3.45	3
9	*Chromis verater*	3.24	2
10	*Pseudocheilinus evanidus*	2.40	2

[1] In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

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[7] Table 6 is based on data from four transects at four outer drop-off sites—two at Palemano Point and two at Puuhonua Point (see Figure 1). Total number of species observed on these four transects: 78; mean number of individuals of all species for a single transect: 478.

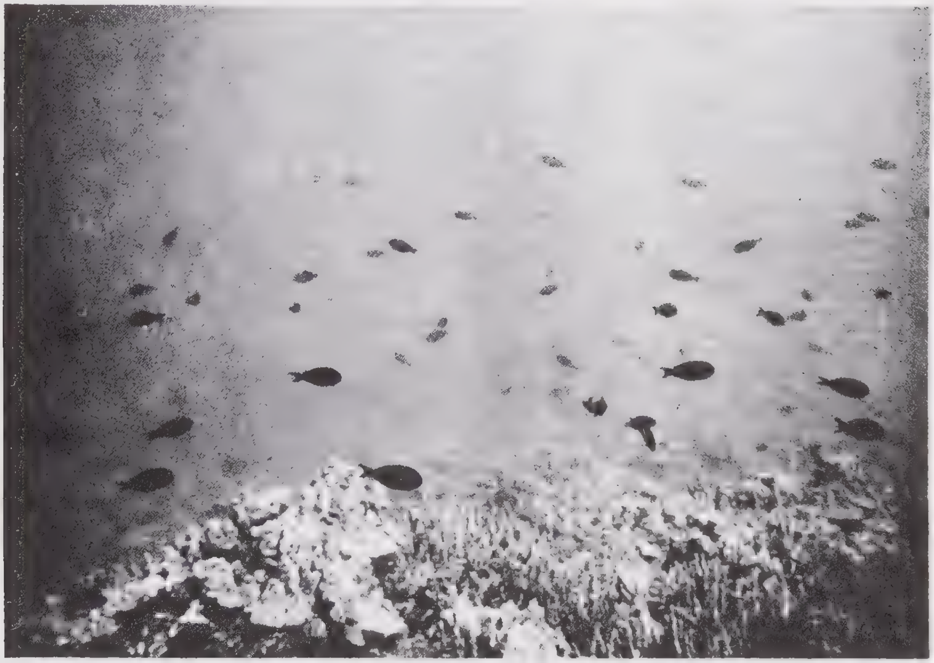


FIGURE 7.—Outer drop-off habitat. Most of the fishes shown in the water column are *Acanthurus thompsoni*.

Fishes Observed on Transect Lines

All fishes observed on transect lines in the five Kona habitats are listed in Table 7, where the value given for each species in each habitat is the relative abundance index, as defined in the methods. Transect data for each habitat category (number of transects, total number of species observed, and mean number of individuals on a single transect) are given in footnotes 2 to 7.

SPECIES ACCOUNTS

Family	*Page*
Muraenidae: moray eels	926
Congridae: conger eels	929
Synodontidae: lizardfishes	929
Brotulidae: brotulas	930
Atherinidae: silversides	931
Holocentridae: squirrelfishes	932
Aulostomidae: trumpetfishes	942
Fistulariidae: cornetfishes	944
Scorpaenidae: scorpionfishes	944
Serranidae: sea basses	947
Kuhliidae: aholeholes	948
Priacanthidae: bigeyes	948
Apogonidae: cardinalfishes	950
Carangidae: jacks	954
Lutjanidae: snappers	955
Sparidae: porgies	956
Mullidae: goatfishes	957
Kyphosidae: sea chubs	964
Chaetodontidae: angelfishes and butterflyfishes	964
Pomacentridae: damselfishes	978
Cirrhitidae: hawkfishes	986
Labridae: wrasses	989
Scaridae: parrotfishes	995
Blenniidae: combtooth blennies	998
Acanthuridae: surgeonfishes	1000
Zanclidae: moorish idol	1003
Bothidae: left-hand flounders	1005
Balistidae: triggerfishes	1005
Monacanthidae: filefishes	1009
Ostraciontidae: boxfishes	1011
Tetraodontidae: balloonfishes	1012
Canthigasteridae: sharp-backed puffers	1013
Diodontidae: spiny puffers	1015

This study treats only teleostean fishes, as these were almost the only kind observed on Kona reefs during this study. Elasmobranchs occurred infrequently and seemed to have little impact on the reef situation. No marine animals are more prominent than sharks in Hawaiian lore (e.g. Hobson and Chave, 1972), yet compared with most other tropical Pacific Islands, relatively few sharks are seen in Hawaiian nearshore waters today.

TABLE 7.—Relative abundance of fish species observed along transect lines in each of the Kona reef habitats.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Superorder Elopomorpha:						
Order Anguilliformes:						
Family Muraenidae:						
Gymnothorax meleagris	—	—	0.04	0.06	—	—
Superorder Protacanthopterygii:						
Order Myctophiformes:						
Family Synodontidae:						
Synodus variegatus	0.04	—	—	—	—	—
Superorder Acanthopterygii:						
Order Beryciformes:						
Family Holocentridae:						
Holocentrus sammara	0.04	0.60	0.04	—	—	0.05
H. tiere	—	0.81	—	—	—	—
H. xantherythrus	—	0.60	—	—	—	—
H. diadema	—	1.01	—	—	—	0.05
H. lacteoguttatum	—	1.21	—	—	—	—
Holotrachys lima	—	0.81	—	—	—	—
Myripristis kuntee	0.23	23.61	0.19	—	0.43	0.26
M. murdjan	0.08	12.33	—	—	0.25	0.31
M. sp. (uncertain: either *M. murdjan* or *M. amaenus*)	—	5.24	—	—	—	—
Order Gasterosteiformes:						
Family Aulostomidae:						
Aulostomus chinensis	0.12	0.40	—	—	0.36	—
Family Fistulariidae:						
Fistularia petimba	—	—	—	0.12	—	—
Order Scorpaeniformes:						
Family Scorpaenidae:						
Taenianotus triacanthus	0.04	—	—	—	—	—
Scorpaena coniorta	—	0.20	—	—	—	—
Scorpaenopsis cacopsis	—	—	—	—	0.07	0.05
Order Perciformes:						
Family Serranidae:						
Cephalapholis argus	—	—	—	—	0.04	—
Family Priacanthidae:						
Priacanthus cruentatus	—	0.20	—	—	—	—
Family Apogonidae:						
Apogon menesemus	—	14.52	—	—	—	—
A. snyderi	—	11.90	—	—	—	—
Family Malacanthidae:						
Malacanthus hoedtii	—	—	—	—	—	0.16
Family Carangidae:						
Caranx melampygus	—	—	0.04	—	0.11	—
Family Lutjanidae:						
Aphareus furcatus	0.15	—	0.11	—	0.21	—
Family Sparidae:						
Monotaxis grandoculis	0.12	—	0.04	—	1.25	0.05
Family Mullidae:						
Mulloidichthys auriflamma	—	—	—	—	0.93	—
M. samoensis	0.12	—	—	—	0.14	—
Parupeneus multifasciatus	0.58	0.20	0.45	0.23	0.82	1.41
P. bifasciatus	0.12	—	0.07	—	0.71	0.05
P. chryserydros	0.27	—	0.15	—	0.25	—
P. porphyreus	0.08	—	—	—	—	—
P. pleurostigma	0.04	—	—	—	—	0.05
Family Kyphosidae:						
Kyphosus cinerascens	—	—	0.22	—	0.11	—
Family Chaetodontidae:						
Holacanthus arcuatus	—	—	—	—	0.11	0.10
Centropyge potteri	2.49	—	—	—	1.00	3.45
C. fisheri	—	—	—	—	—	0.16
Forcipiger flavissimus	0.96	—	1.01	0.35	0.78	1.41
F. longirostris	0.50	0.40	—	0.12	0.07	0.31
Hemitaurichthys thompsoni	—	0.40	—	—	—	0.73
H. zoster	—	—	0.26	—	—	2.09
Chaetodon corallicola	—	—	—	—	—	1.05
C. miliaris	—	—	—	—	—	1.05
C. quadrimaculatus	0.69	—	0.89	1.44	0.53	0.10
C. unimaculatus	—	—	0.22	1.21	—	—
C. multicinctus	4.41	4.03	1.08	0.58	0.82	3.76
C. ornatissimus	1.80	1.21	0.68	0.29	0.25	0.31
C. auriga	—	—	—	—	0.04	0.05
C. fremblii	0.08	0.20	0.30	0.12	0.32	0.05
C. lunula	0.69	1.21	0.15	0.40	2.03	0.58
C. lineolatus	—	0.20	0.11	—	0.11	—

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
C. reticulatus	—	—	—	0.12	—	—
C. trifasciatus	0.04	—	—	0.12	—	—
Family Pomacentridae:						
Plectroglyphidodon johnstonianus	3.07	0.20	0.07	1.04	0.25	1.25
Pomacentrus jenkinsi	6.71	—	5.25	1.67	3.95	0.68
Abudefduf sindonis	—	—	3.64	—	—	—
A. sordidus	—	—	0.22	—	0.39	—
A. imparipennis	—	—	0.22	15.12	—	—
A. abdominalis	0.35	0.20	—	—	3.56	—
Dascyllus albisella	0.19	1.21	0.07	—	—	2.30
Chromis vanderbilti	0.15	—	2.35	10.33	11.74	0.84
C. leucurus	12.30	—	—	—	0.82	11.19
C. verater	0.96	0.80	0.11	—	0.14	3.24
C. ovalis	0.11	0.40	—	—	—	—
Family Cirrhitidae:						
Paracirrhites arcatus	0.69	—	0.74	0.86	0.89	0.99
P. forsteri	0.23	—	—	0.12	0.11	—
Cirrhitops fasciatus	0.12	—	0.34	0.17	0.82	0.47
Cirrhitus pinnulatus	0.04	—	—	0.52	0.18	0.05
Family Labridae:						
Bodianus bilunulatus	—	—	—	—	—	0.05
Cheilinus rhodochrous	1.57	—	0.15	—	0.57	1.41
Pseudocheilinius octotaenia	1.30	—	0.07	—	0.82	1.93
P. tetrataenia	0.31	—	0.04	0.23	0.07	0.42
P. evanidus	0.04	—	—	—	—	2.40
Labroides phthirophagus	0.31	—	—	—	—	0.05
Thalassoma duperrey	5.71	—	6.44	17.41	4.41	6.64
T. fuscus	—	—	1.97	4.78	—	—
T. ballieui	0.04	—	0.15	0.17	0.21	0.05
T. lutescens	0.08	—	—	—	—	—
T. quinquevittata	—	—	—	0.23	—	—
Halichoeres ornatissimus	1.15	—	1.67	0.58	0.53	1.15
Stethojulis balteata	2.15	—	1.56	2.88	1.35	0.68
Anampses cuvier	0.08	—	0.34	0.06	0.07	0.05
Coris gaimard	0.81	—	0.26	0.35	0.71	1.31
C. flavovittata	—	—	—	—	0.04	—
C. venusta	—	—	—	—	0.11	—
Macropharyngodon geoffroy	0.15	—	0.07	0.52	0.21	0.73
Gomphosus varius	1.00	—	1.53	2.78	0.60	0.78
Cirrhilabrus jordani	—	—	—	—	—	0.16
Pseudojuloides cerasinus	—	—	—	—	—	0.05
Hemipteronotus taeniourus	—	—	—	—	—	0.16
Family Scaridae:						
Scarus sordidus	1.73	—	0.82	1.04	1.81	1.93
S. taeniurus	0.19	—	0.63	0.98	0.43	—
S. dubius	0.46	—	0.52	—	0.50	0.16
S. perspicillatus	0.35	0.20	1.53	—	0.28	0.10
S. rubroviolaceus	0.35	0.20	0.04	0.29	0.50	0.10
Calotomus spinidens	0.50	—	0.04	0.12	0.11	0.26
Unidentified juveniles	—	—	—	—	0.89	—
Family Blenniidae:						
Exallias brevis	0.15	—	0.11	0.06	0.11	0.05
Cirripectus obscurus	—	—	0.15	—	—	—
C. variolosus	0.31	—	0.04	—	0.07	—
Plagiotremus goslinei	—	—	0.19	0.98	0.04	—
P. ewaensis	—	—	—	—	0.04	—
Family Acanthuridae:						
Acanthurus achilles	0.69	1.41	8.00	0.35	3.56	0.10
A. dussumieri	0.35	—	0.74	—	0.28	—
A. glaucopareius	0.04	—	0.19	—	0.07	—
A. guttatus	—	—	1.64	—	—	—
A. leucopareius	0.69	1.01	4.73	0.40	7.18	—
A. nigrofuscus	4.37	0.40	13.74	20.23	6.17	1.62
A. nigroris	3.64	2.22	4.88	1.38	1.60	1.57
A. olivaceus	0.19	—	0.11	—	0.07	0.31
A. sandvicensis	0.12	2.40	1.64	0.12	0.71	—
A. thompsoni	—	—	—	—	—	1.88
A. xanthopterus	—	—	—	—	0.43	—
Ctenochaetus strigosus	15.45	—	10.77	—	9.54	3.87
C. hawaiiensis	0.58	—	0.82	—	0.75	0.05
Zebrasoma flavescens	10.58	6.85	9.61	1.79	9.11	4.76
Z. veliferum	0.15	—	0.22	—	—	—
Naso brevirostris	—	—	—	—	—	0.10
N. hexacanthus	—	—	—	—	1.28	11.39
N. lituratus	1.46	1.21	0.74	2.02	1.07	1.20
N. unicornis	0.35	—	0.60	1.50	0.25	0.05

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Family Zanclidae:						
Zanclus canescens	0.38	—	1.38	1.21	0.82	1.10
Order Tetraodontiformes:						
Family Balistidae:						
Melichthys niger	1.00	—	0.82	0.12	3.38	—
M. vidua	0.04	—	—	—	—	0.15
Xanthichthys ringens	—	—	0.04	—	0.39	10.50
Rhinecanthus rectangulus	—	—	0.19	1.33	—	—
Sufflamen bursa	0.73	—	0.37	—	1.57	1.57
Balistid sp.	—	—	—	—	0.04	—
Family Monacanthidae:						
Cantherines dumerili	0.15	—	—	0.12	0.11	—
C. sandwichiensis	0.15	—	0.40	0.64	0.32	0.16
Pervagor spilosoma	0.35	—	—	—	0.04	0.10
P. melanocephalus	0.42	—	0.19	—	—	0.10
Alutera scripta	—	—	—	—	0.04	—
Family Ostraciontidae:						
Ostracion meleagris	0.19	—	0.86	0.12	0.18	—
Family Tetraodontidae:						
Arothron hispidus	—	—	—	—	0.04	—
A. meleagris	—	—	0.04	0.06	—	—
Family Canthigasteridae:						
Canthigaster amboinensis	0.12	—	0.22	0.17	0.11	—
C. jactator	0.46	—	0.04	—	0.78	0.05
C. coronatus	—	—	—	—	0.04	0.10

The observations for each species are grouped by order and family in phylogenetic sequence, as listed by Greenwood et al. (1966). Species names generally are those used by Gosline and Brock (1960), except where more recent taxonomic studies indicate change. All sizes given are standard length. For most species, the number of specimens collected is followed by, in parenthesis, their mean size and the range in their sizes. All species accounts consider individuals showing morphology and behavior of adults.

ORDER ANGUILLIFORMES

Family Muraenidae: moray eels

Most Hawaiian eels belong to this family, which comprises the moray eels, or *puhi*, as Hawaiians call them (Gosline and Brock, 1960). Morays are denizens of crevices in the reefs, and because most remain secreted under cover, their great abundance cannot be appreciated by a casual observer. Nevertheless, the morays include more species (32 reported) on Hawaiian reefs than any other family of fishes, except perhaps the wrasse family Labridae (Gosline and Brock, 1960). Most Hawaiian morays do not grow to more than about 60 cm long, although a few may attain a length of about 2 m (Gosline and Brock, 1960). Most of them remain secreted in reef crevices, but the five species considered below are examples of those that are often exposed on the reef top.

Gymnothorax meleagris (Shaw and Nodder) —spotted moray, *puhi 'oni'o*

This medium-sized eel characteristically protrudes its head from crevices during the day (Figure 8), and thus is the moray most often in view on the reef; however, I seldom saw it after dark. Of the nine specimens collected, the stomachs of five were empty, although three of these contained unidentified fragments at the posterior end of their intestines. Of the four with prey in their stomachs, one (455 mm) taken during midmorning contained a fresh damselfish, *Abudefduf imparipennis* (40 mm) that appeared to have been recently captured. Two others with full stomachs were collected during late afternoon: one (321 mm) contained a moderately digested xanthid crab, whereas the other (121 mm) contained a well-digested fish. On the other hand, the fourth specimen (361 mm) contained a moderately digested xanthid crab that appeared to have been in the eel's stomach at least several hours when it was collected during morning twilight.

CONCLUSION.—*Gymnothorax meleagris* captures small fishes and crustaceans by day and probably also at night.

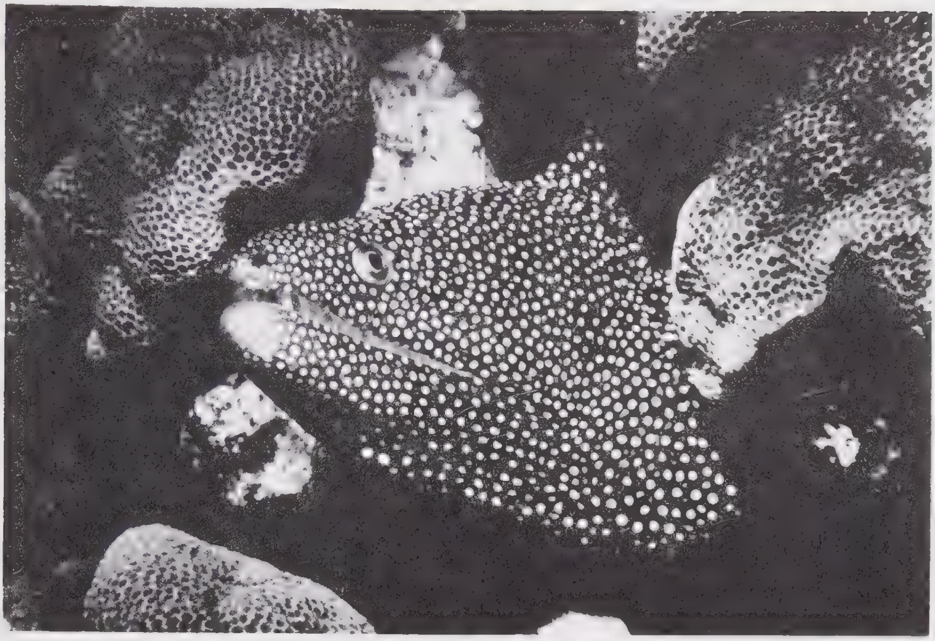


FIGURE 8.—*Gymnothorax meleagris*, a moray eel, showing daytime attitude.

Gymnothorax eurostus (Abbott)

This small species, which attains a maximum length of about 60 cm, is probably the most numerous moray in Hawaii (Gosline and Brock, 1960). However, it is a secretive species, only occasionally visible on the reef. Although the four individuals collected (360: 294-432 mm) were speared as they protruded their heads from holes in the reef during the day, this habit is not characteristic of *G. eurostus*, as it is of *G. meleagris*, above. Two of those collected had empty stomachs, but the other two, both taken during midday, contained relatively fresh prey—a caridean shrimp in one, a xanthid crab in the other.

CONCLUSION.—*Gymnothorax eurostus* captures crustaceans during the day. The nighttime situation remains uncertain.

Gymnothorax flavimarginata (Rüppell)—*puhi paka*

This eel, which attains a length of about 120 cm (Gosline and Brock, 1960), is the most numerous of the larger muraenids in Kona. Being so abundant, as well as large, this heavy-bodied eel probably represents the greatest threat among morays to humans. It is the species that most often appears when a fish has been speared during daylight. The regularity and promptness of these appearances make it clear that *G. flavimarginata* is especially sensitive to fish that are injured, or perhaps otherwise under stress. In this respect it is similar to *G. castaneus* in the Gulf of California (Hobson, 1968a). Usually when a reef fish is injured, or seriously threatened, it takes cover in a reef crevice. Usually such individuals are to some extent incapacitated, and thus vulnerable to predators equipped to seek them out. Probably *G. flavimarginata* is adapted to this task. Other large morays on the reef show the same behavior, but to a lesser degree. Most encounters with *G. flavimarginata* were by day; although its behavior would seem equally adaptive to nocturnal conditions, it was only occasionally observed after dark.

CONCLUSION.—*Gymnothorax flavimarginata* is especially sensitive to stimuli emanating from a fish in distress, and appears adapted to seeking out such individuals when they have sought shelter in reef crevices.

Gymnothorax petelli (Bleeker)—broad-banded moray

The broad-banded moray generally is out of sight within the reef during daylight, but often active in exposed locations after dark (Figure 9). A second species, *G. undulatus,* similarly forays away from cover at night, but during this study was seen less often than *G. petelli.* Although no specimens were examined, one *G. petelli* seen on the reef at night was grasping between its jaws a pufferfish, *Canthigaster jactator.* Additional evidence of nocturnal habits in *G. petelli* was given by Chave and Randall (1971), who described it pursuing crabs over underwater sand patches at night.

CONCLUSION.—*Gymnothorax petelli* is a nocturnal predator.

Echidna zebra (Shaw)—zebra moray

The zebra moray has a blunter snout than the species of *Gymnothorax* treated above, but its dentition is even more distinctive. Morays of the genus *Gymnothorax* have fanglike teeth that are suited to grasping prey, but the zebra moray, like other species of the genus *Echidna,* has blunt, pebblelike teeth that are suited to crushing prey. Gut contents are consistent with this observation: all four specimens (750: 485-835 mm) taken at various times of the day contained the crushed remains of relatively large crabs—considerably larger than crabs found in comparably sized individuals of *Gymnothorax.* The zebra moray is a sluggish animal, even for a moray, and is generally secretive. Usually all one sees of this animal, day or night, is a motionless segment of its body, visible at a narrow opening in the reef.

CONCLUSION.—*Echidna zebra* captures crustaceans within reef crevices, taking larger individuals of the more heavily armored prey than do species of *Gymnothorax.*

General Remarks on Moray Eels

Morays have been widely considered, collectively, as nocturnal animals (e.g. Winn and Bardach, 1959; Starck and Davis, 1966; Randall,

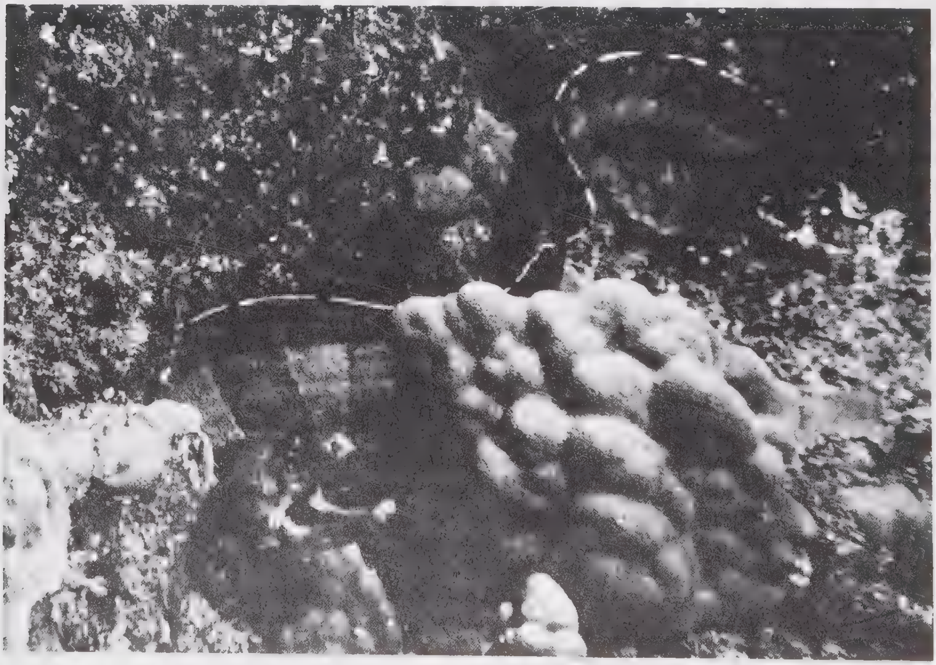


FIGURE 9.—*Gymnothorax petelli,* a moray eel, on the reef top at night.

1967; Collette and Talbot, 1972). Hiatt and Strasburg (1960) attributed the high incidence of empty stomachs in morays from the Marshall Islands during daylight to nocturnal habits; however, I concur with Gosline and Brock (1960), who attributed the empty stomachs of Hawaiian morays during the day to infrequent feeding, rather than necessarily to nocturnal feeding. Certainly some morays seem to be primarily nocturnal—*Gymnothorax petelli* and *G. undulatus*, described above, are examples. But others described here, such as *G. meleagris, G. eurostus,* and *G. flavimarginata,* feed regularly in daylight. That some morays are primarily diurnal was illustrated by Chave and Randall (1971), who described a diurnally active, nocturnally inactive pattern for *G. pictus* in the central Pacific. Conclusions on relative activity between day and night for moray eels remain tenuous if based solely on how often, and at what time, the species is seen in exposed positions. Moray eels are adapted to activity within reef crevices, and one would expect at least most of them to best capture their prey there; indeed, most species rarely expose themselves, day or night.

Family Congridae: conger eels

Conger marginatus Valenciennes—white eel, *puhi uha*

The white eel, which may exceed a length of 1 m (Gosline and Brock, 1960), is relatively numerous in Kona. It moves about in the open on the reef after dark and rests in reef crevices during daylight. In the Marshall Islands, Hiatt and Strasburg (1960) reported similar behavior in *C. noordzieki*, which preys on both fishes and invertebrates.

CONCLUSION.—*Conger marginatus* is active in exposed locations on the reef after dark.

ORDER MYCTOPHIFORMES

Family Synodontidae: lizardfishes

Saurida gracilis (Quoy and Gaimard)–*'ulae nihoa*

Attaining lengths of over 300 mm, this is the largest of those lizardfishes that are numerous on the reef. During both day and night it rests motionless and fully exposed on sand patches, rock, or coral. Despite these exposed positions, it is difficult to detect, so closely does its coloration match the surroundings. Six specimens (223: 165-315 mm) were examined. The guts were empty in five—four speared at night, between 2300 h and dawn, and one taken during midday. The sixth specimen (165 mm), taken 1 h before midnight, contained the well-digested anterior half of a trumpetfish, *Aulostomus chinensis* (about 90 mm when intact). Because digestion was far advanced, this prey may have been ingested during the previous day or evening twilight. These limited data suggest that attacks are infrequent, or perhaps that feeding habits are diurnal or crepuscular. Hiatt and Strasburg (1960) reported strictly piscivorous habits for this species in the Marshall Islands, and described daylight attacks in which it darted upward from a resting spot on the sea floor.

CONCLUSION.—*Saurida gracilis* attacks small fishes in daylight.

Synodus variegatus (Lacépède)—*'ulae 'ula*

This is the most numerous synodontid on Kona reefs. During both day and night it rests on the sea floor (Figure 10), as does *Saurida gracilis,* above. Although usually in exposed positions, it is difficult to detect because its coloration closely matches the background. Frequently it becomes even more inconspicuous by burying in the sand, leaving only its eyes and the tip of its snout exposed.

Once, during early afternoon, an individual of this species shot up from the coral and captured a small wrasse, *Thalassoma lutescens,* that I was stalking. The wrasse was watching me when the lizardfish struck, and the attacker may have sensed this distraction in its prey. I speared the predator immediately after the attack, and found it to be 166 mm long (it lost the wrasse when speared and is included below among those with an empty gut). Two other noteworthy incidents occurred at night: On both occasions I was hunting specimens among the coral, and my spear, projecting into my path, was faintly illuminated by my companion's diving light. Suddenly, an individual of this species darted up and struck the silver barb on the otherwise grey spear. Although the nearby diving light created here an unnatural nocturnal situation, these two fish obviously were alert for prey at these times.

Twelve specimens (142: 94-158 mm) were collected during day and night from exposed posi-

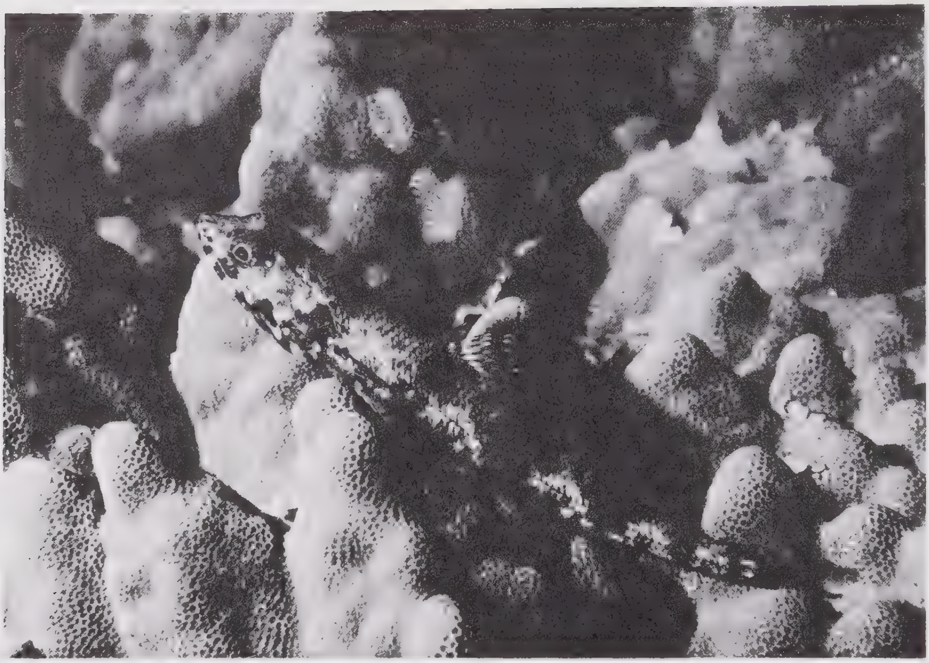


FIGURE 10.—*Synodus variegatus,* a lizardfish, poised to strike at prey in the water overhead.

tions on the sea floor. Of nine speared during afternoons, six had empty guts, but two contained fish fragments, and one contained three fish—two digested beyond recognition, and one relatively fresh *Plagiotremus goslinei* (32 mm). Of two collected during morning twilight, one was empty, while the other contained an extensively digested fish (25 mm). Finally, one collected at night, 5 h after sunset, contained fish fragments.

CONCLUSION.—*Synodus variegatus* attacks small fishes during the day and probably also at night.

General Remarks on Lizardfishes

Similar behavior is widely reported for the synodontids of tropical seas. In the Florida Keys, Starck and Davis (1966) reported that *Synodus synodus* and *Trachinocephalus myops* lie partially buried in the sand and erupt to capture prey swimming overhead during the day. Similarly, Randall (1967) noted that lizardfishes in the West Indies, including *S. synodus, S. intermedius,* and *S. foetens,* may rest on rocks, sand, or mud, where they sometimes partially bury themselves. Hartline et al. (1972) observed on several occasions during the day *Synodus* sp. in the Virgin Islands attacking the damselfish *Chromis cyaneus* from resting positions on the substratum. Similar observations were also reported by Smith and Tyler (1972). Although fishes seem to be the major prey of synodontids, Randall (1967) found some shrimps and squids in the predominantly piscivorous diet of lizardfishes in the West Indies. Suyehiro (1942) also reported shrimps and squid secondary prey to fishes in the diet of *Saurida undosquamis* in Japan. Probably any free-swimming animal of appropriate size becomes prey if it passes close above a waiting lizardfish when conditions are suitable for attack. The jaws of lizardfishes are profusely rimmed with sharp, inwardly depressible canine teeth, like those of many morays, and this type of dentition is especially well suited to grasping small fishes.

ORDER GADIFORMES

Family Brotulidae: brotulas

Brotula multibarbata Temminck and Schlegel—*puhi palahoana*

This fish is not in view during daylight, except to one who enters some of the darker caves. Although diurnally secretive, it swims into the open on the reef after dark, but even then is mostly exposed only during transit from one crevice to another.

Seven individuals (169: 73-250 mm) were speared during day and night. Two collected about 2 h before daybreak as they swam close among rocks were both full of prey, including fresh material. Of three others collected in dark caves during midmorning, one was empty and the other two contained only well-digested fragments. Finally, two individuals collected within 1 h after nightfall as they swam in exposed locations among rocks were both empty—apparently having not yet captured prey on their nocturnal foray. The four individuals containing identifiable prey had fed on the items listed in Table 8.

CONCLUSION.—*Brotula multibarbata* is a nocturnal predator that feeds mostly on crustaceans and fishes.

General Remarks on Brotulas

Hiatt and Strasburg (1960) concluded that *Dinematichthys ilucoeteoides* in the Marshall Islands is very secretive because they never saw a live one, but did not suggest that it might be nocturnal. They believed that by concealing itself in crevices this brotulid is able to dash out and capture small fishes and crustaceans that unsuspectingly venture close to its hiding place. Starck and Davis (1966) recognized nocturnal habits in an Atlantic species, *Petrotyx sanguineus,* which is unseen in daylight, but swims close among reef ledges at night.

ORDER ATHERINIFORMES

Family Atherinidae: silversides

Pranesus insularum (Jordan and Evermann)—*'iao*

This silverside is not numerous in Kona, but in daylight small schools of relatively inactive individuals occur at various places along the rocky shore, right at the water's edge. At nightfall these schools disperse, and the members move away from shore, over the reef. They swim high in the water column, just under the water surface, and some of them range out at least as far as the offshore drop-off.

Using a hard net, 13 individuals (47: 39-70 mm) were collected during both dark nights and moonlit nights—9 between 4 and 6 h after sunset and 4 during the 2 h before first morning light. Although the gut of 1 was empty, the other 12 were full, including fresh material, as listed in Table 9.

CONCLUSION.—*Pranesus insularum* is a nocturnal planktivore that takes mostly crustaceans and foraminiferans.

TABLE 8.—Food of *Brotula multibarbata.*

Rank	Items	No. fish with this item (*n* = 4)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	1	25.0	6.25
2	Fish	1	16.3	4.08
3	Decapod shrimps	1	6.3	1.58
4	Mysids	1	5.0	1.25
5	Crab megalops	1	0.3	0.08
Also, crustacean fragments		2	37.5	18.75
	Unidentified fragments	3	9.6	7.20

TABLE 9.—Food of *Pranesus insularum.*

Rank	Items	No. fish with this item (*n* = 12)	Mean percent of diet volume	Ranking index
1	Mysids	5	14.2	5.92
2	Decapod shrimp larvae	5	6.7	2.79
3	Foraminiferans	4	6.3	2.10
4	Calanoid copepods	2	4.2	0.70
5	Larvaceans	1	2.1	0.18
6	Crab zoea	1	1.7	0.14
7	Spider	1	0.4	0.03
Also, crustacean fragments		12	40.8	40.80
	Unidentified fragments	7	23.6	13.79

General Remarks on Silversides

It is widely recognized that silversides prey largely on zooplankton. Hiatt and Strasburg (1960) found mostly zooplankton in three species in the Marshall Islands, as did Randall (1967) in two species from the West Indies. Each report listed shrimp larvae and copepods among the major food items, but neither mentioned nocturnal habits. At Majuro Atoll, Marshall Islands, *Pranesus pinguis* is inactive in schools along lagoon beaches during the day, and then migrates offshore into the lagoon at nightfall, where it disperses and feeds on zooplankton in the surface waters (Hobson and Chess, 1973). The closely related *P. insularum* does not move so far from shore at night in Kona, presumably because its feeding grounds are over the nearshore reefs.

ORDER BERYCIFORMES

Family Holocentridae: squirrelfishes

The squirrelfishes compose one of the more prominent groups of fishes on Hawaiian reefs. The species fall into two major categories: those in one group include members of the genus *Holocentrus,* which are known by the generic Hawaiian name *ala 'ihi,* and one species of the genus *Holotrachys*; those in the second group include species of the genus *Myripristis,* which are known by the generic Hawaiian name *'u'u,* or perhaps more often today by the Japanese equivalent *menpachi.*

Holocentrus sammara (Forskål)

This solitary fish is numerous in coral-rich surroundings at depths between 4 and 20 m. It is a relatively large species—up to 300 mm long (Gosline and Brock, 1960)—and characteristically hovers in visible locations at the openings of reef caves during the day. During evening twilight it moves away from its daytime shelter-sites and throughout the night ranges over the nearby areas of the reef, staying close to the sea floor. During morning twilight it gradually moves closer to cover and by sunrise has resumed its daytime mode of behavior. After dark the coloration of this fish differs from its coloration in daylight (Figure 11a and b).

Twenty-one specimens (162: 128-202 mm) were collected during day and night for food-habit study. All 13 that were speared as they swam in exposed positions on the reef during the last hours of darkness, before daybreak, and during morning twilight contained prey in varying stages of digestion. In comparison, of seven speared as they hovered close among coral shelter during the afternoon, four were empty, two contained only well-digested fragments, and one contained an apparently recently ingested crab. Finally, one that was speared in the open 4 h after nightfall was full of prey, most of it fresh. Items in the 17 specimens containing identifiable material are listed in Table 10.

CONCLUSION.—*Holocentrus sammara* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps, but some feed diurnally.

Holocentrus spinifera (Forskål)

This is the largest squirrelfish on Kona reefs, and of those considered in this report it is also the least numerous. A solitary species during both day and night, it is secretive within reef crevices in daylight, but ranges out and forages close to the reef after dark. In daylight, the body of this fish is a plain rosy-red, and its dorsal fin is yellow; in darkness, however, a small but prominent white spot appears on each side of its body, just behind its dorsal fin. Because this large fish is not numerous, I came to recognize certain individuals and found that after nocturnal forays on the reef each tended to return each morning to its particular shelter spot.

Six specimens (213: 68-350 mm) were speared during day and night for study of food habits. The one that was taken during midday contained a large caridean shrimp, *Saron marmoratus* (about 40 mm), that was extensively damaged by digestion and could have been taken during the previous night. A second, taken as it emerged from cover at nightfall, was the only one taken with an empty gut. Of the other four, all of which contained relatively fresh prey, three were collected as they swam in the open at night, more than 3 h after sunset, and the fourth was collected under a ledge during morning twilight.

All five specimens containing food had fed on crustaceans exclusively. Three had taken caridean shrimps (mean percent of diet volume: 34; ranking index: 20.4), three had taken xanthid crabs (mean percent of diet volume: 31; ranking index: 18.6), and one had taken a scyllarid lobster (mean percent of diet volume: 11; ranking index:

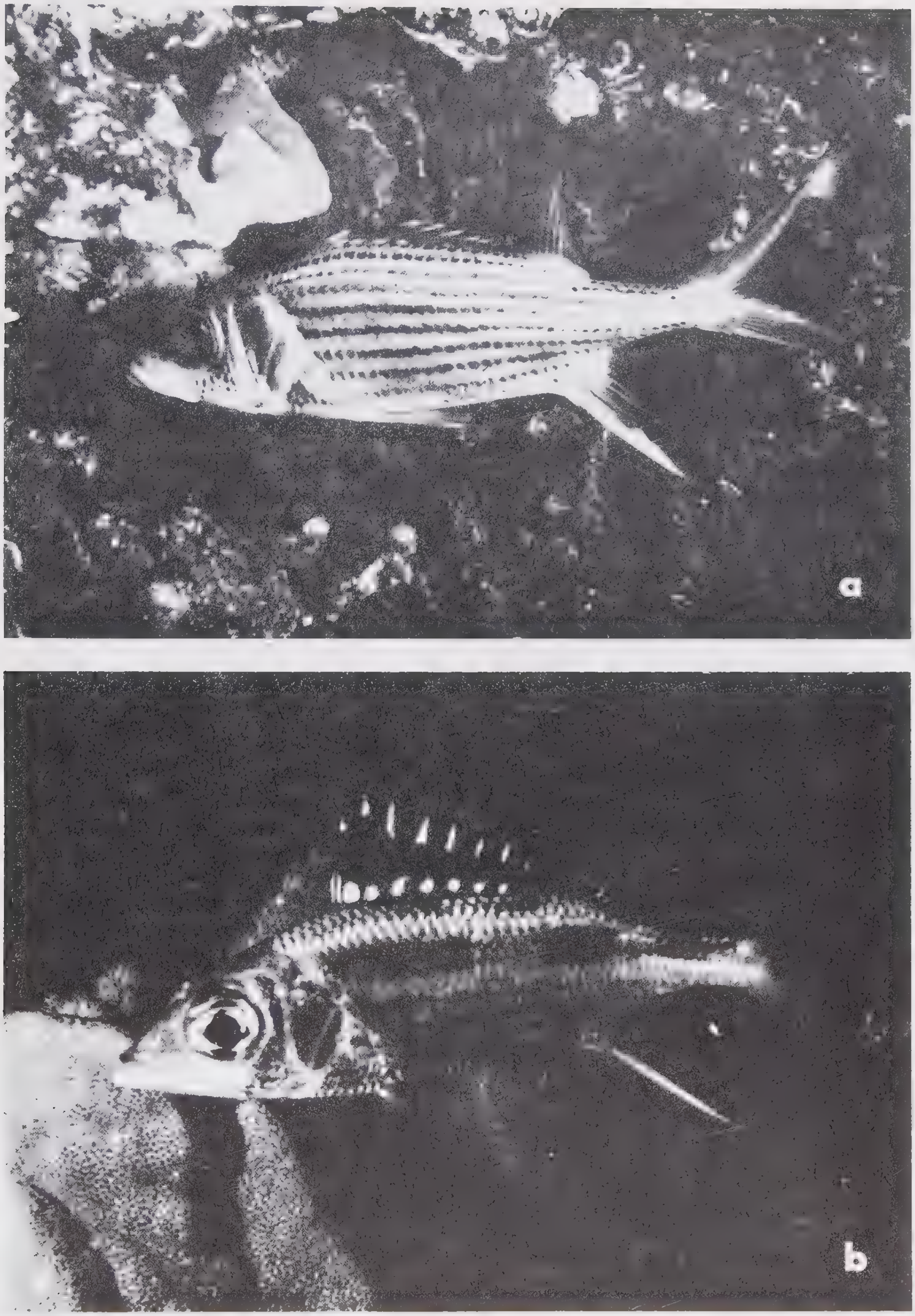


FIGURE 11.—*Holocentrus sammara,* a squirrelfish: a, showing its diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 10.—Food of *Holocentrus sammara.*

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	52.5	37.08
2	Caridean shrimps	4	12.2	2.88
3	Portunid crabs	2	7.8	0.92
4	Fish	2	7.8	0.92
5	Penaeid shrimps	1	5.9	0.35
Also, crustacean fragments		4	13.8	3.25

2.2). Three contained unidentified crustacean fragments (mean percent of diet volume: 24; ranking index: 14.4).

CONCLUSION.—*Holocentrus spinifera* is a nocturnal predator that feeds mostly on benthic crustaceans, especially caridean shrimps and xanthid crabs.

Holocentrus tiere Cuvier

This relatively numerous holocentrid is mostly secreted in reef caves during the day, but after dark swims in exposed locations at depths below 5 m, especially along reef ledges. It emerges from cover after last evening light and regains shelter before, or at, first morning light. Like *H. sammara* and *H. spinifera,* above, *H. tiere* has distinctive diurnal and nocturnal color patterns (Figure 12a and b).

Fifteen specimens (141: 67-160 mm) were speared as they swam in the open at night, or just after they had returned to shelter at daybreak: 11 of these had food in their stomachs; 3 taken within 4 h after sunset were empty—apparently their nocturnal hunt had not yet been successful; 1 taken under a ledge during morning twilight also had an empty gut, indicating that it had passed the night without feeding. Items in the 11 specimens containing identifiable material are listed in Table 11.

CONCLUSION.—*Holocentrus tiere* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps.

Holocentrus xantherythrus Jordan and Evermann

During the day this relatively small holocentrid aggregates in crevices and under overhangs of basalt reefs (Figure 13) in water deeper than 6 m, but especially below 20 m. After dark it ranges out from this shelter and into the surrounding areas, where solitary individuals are active close to rock, coral, or pockets of sand. By first morning light it has returned to its daytime retreats. At night this fish has prominent white vertical markings on its body like those illustrated for *H. tiere* (Figure 12b).

Of the 29 individuals (106: 88-123 mm) speared at different times of day and night, the stomachs of all 15 that were active in exposed locations on the reef during the 2 h immediately before daybreak, or were under reef shelter within an hour of sunrise, contained prey in varying stages of digestion, whereas the stomachs of all 11 taken from reef crevices during afternoons were empty. The remaining three were taken within 2 h after last light, shortly after they had begun their nightly foraging, and although one was empty, the other two contained fresh prey. Items in the 17 specimens that contained identifiable material are listed in Table 12.

CONCLUSION.—*Holocentrus xantherythrus* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming crustaceans are also taken close to the bottom.

Holocentrus diadema Lacépède

After dark, many individuals of this relatively small squirrelfish swim close to the sea floor where coral growth is rich at depths below 3 to 4 m. *Holocentrus diadema* is secretive by day, generally remaining out of sight within the many narrow interstices of its coral-rich habitat, but is occasionally glimpsed in the shadows at the base of coral heads. Generally, it does not leave its daytime shelter until after last evening light, and returns to cover before or at first morning light. At night this fish, like *H. xantherythrus,* above, has prominent white vertical markings on its body that are similar to those on the nocturnally active *H. tiere* (Figure 12b).

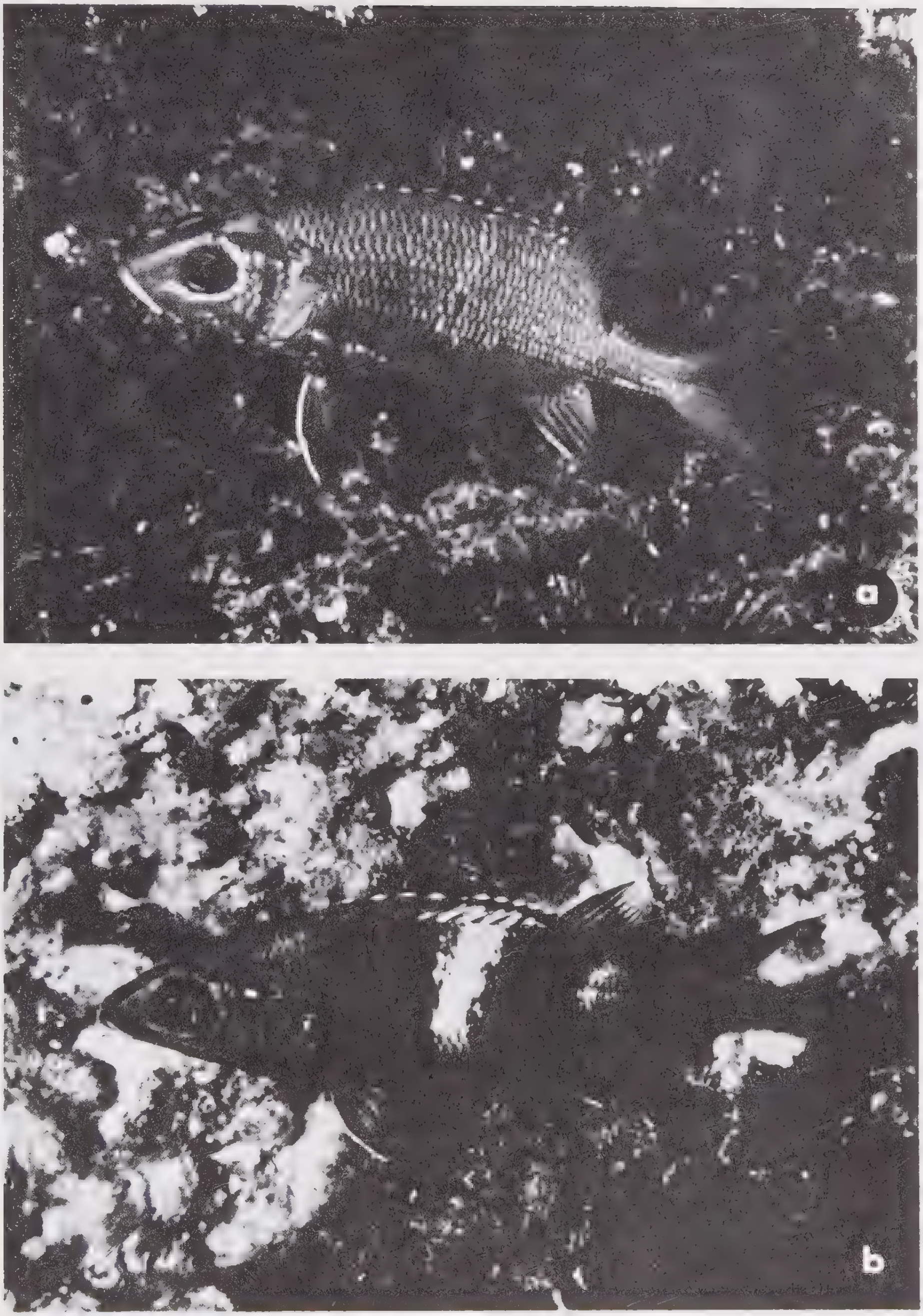


FIGURE 12.—*Holocentrus tiere,* a squirrelfish: a, showing diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 11.—Food of *Holocentrus tiere.*

Rank	Items	No. fish with this item (*n* = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	8	38.7	28.15
2	Caridean shrimps	5	24.7	11.23
3	Crab megalops	5	4.8	2.18
4	Fish	1	1.8	0.16
5	Polychaetes	1	0.2	0.02
6	Sipunculid introverts	1	0.1	<0.01
Also, crustacean fragments		8	29.7	21.60

TABLE 12.—Food of *Holocentrus xantherythrus.*

Rank	Items	No. fish with this item (*n* = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	42.3	29.86
2	Crab megalops	11	14.8	9.58
3	Caridean shrimps	7	15.1	6.22
4	Prosobranch gastropods	4	2.3	0.54
5	Stomatopods	2	1.9	0.22
6	Opisthobranch gastropods	1	0.9	0.05
7	Sipunculid introverts	1	0.8	0.05
8	Pelecypods	1	0.6	0.04
9	Euphausiids	1	0.3	0.02
10	Oxyrhynchid crabs	1	0.3	0.02
11	Tanaids	2	0.2	0.02
12	Flabelliferan isopods	1	0.1	0.01
13	Mysids	1	0.1	0.01
Also, crustacean fragments		10	20.3	11.94

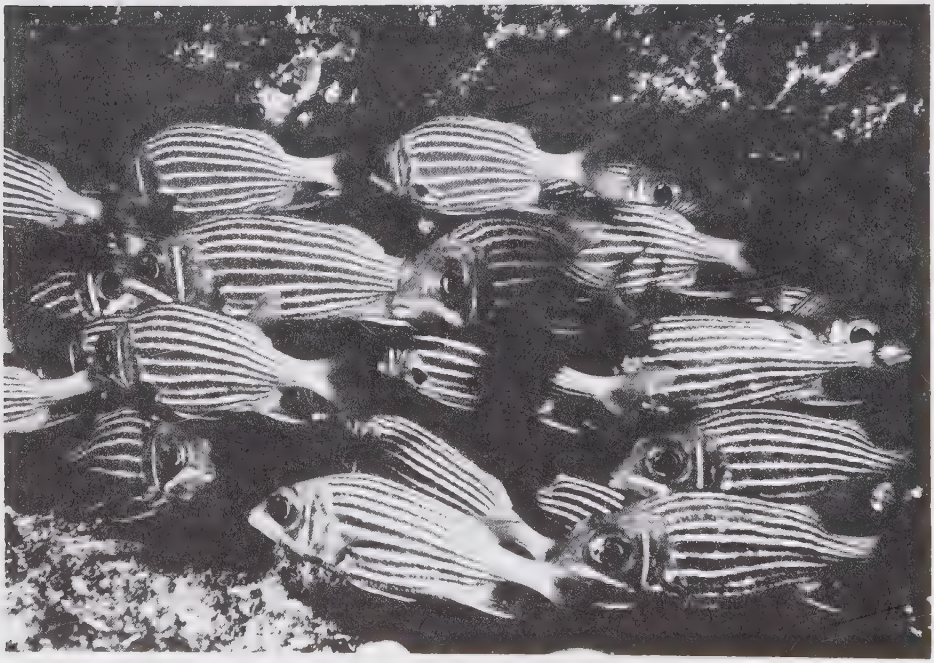


FIGURE 13.—*Holocentrus xantherythrus*, a squirrelfish, aggregated under a ledge during the day.

TABLE 13.—Food of *Holocentrus diadema*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	17	26.7	17.46
2	Ophiuroids	12	12.0	5.54
3	Crab megalops	11	12.4	5.25
4	Caridean shrimps	11	9.7	4.10
5	Prosobranch gastropods	13	6.2	3.10
6	Polychaetes	6	6.1	1.41
7	Gammaridean amphipods	5	1.7	0.33
8	Penaeid shrimps	2	2.3	0.18
9	Isopods	3	1.4	0.16
10	Chitons	1	1.7	0.07
11	Mysids	2	0.8	0.06
12	Portunid crabs	1	0.8	0.03
13	Holothurians	1	0.6	0.02
14	Oxyrhynchid crabs	1	0.4	0.02
15	Tanaids	1	0.4	0.02
16	Calanoid copepods	1	0.4	0.02
17	Pelecypods	1	0.4	0.02
18	Opisthobranch gastropods	1	0.2	0.01
19	Echinoids	1	0.2	0.01
20	Harpacticoid copepods	1	0.1	<0.01
21	Limpets	1	0.1	<0.01
Also,	crustacean fragments	15	11.3	6.63
	Unidentified fragments	4	3.9	0.60

Twenty-eight specimens (109: 85-127 mm) were speared as they swam in exposed locations on the reef at various times during the night. Only two had empty stomachs: in one of these, taken shortly after nightfall, the entire gut was empty, which indicated it had not as yet hunted successfully that night; the other, taken with an empty stomach just before daybreak, had a full intestine, suggesting that it had fed early but not late during the night. The other 26 specimens all contained food in varying stages of digestion, most of it identifiable, as listed in Table 13.

CONCLUSION.—*Holocentrus diadema* is a nocturnal predator that feeds mostly on benthic crustaceans, although it also takes free-swimming forms close to the bottom.

Holocentrus lacteoguttatum Cuvier

This small squirrelfish is similar to *H. xantherythrus* and *H. diadema,* but frequents shallower water than the other two, being most numerous during the day in rocky crevices along surge-swept shores, often where the water is only 1 to 4 m deep. It aggregates in these crevices, and after nightfall ranges out over coral, rock, or pockets of sand on the surrounding reef. Gosline and Brock (1960) also noted the shallowwater habits of this species, but in at least some situations it occurs in depths below 30 m (Gosline, 1965). These habitat distinctions are clearest in daylight, when the three species have retired to their shelters. The differences are less clear at night, when their activity ranges overlap. *Holocentrus lacteoguttatum* does not seem to have prominent nocturnal color features, as do certain other species of *Holocentrus,* treated above; however, several individuals after having been speared at night showed faint traces of essentially the same white markings characteristic of nocturnally active individuals of *H. xantherythrus, H. diadema,* and *H. tiere* (see Figure 12b).

Twenty-one specimens (88: 52-104 mm) were collected at various times of day and night. All but 1 of 13 active individuals that were speared in the open at night (more than 4 h after sunset and before they had returned to shelter at daybreak) had food in their stomachs; the lone exception, collected 4 h after sunset, had a completely empty gut, indicating it had not yet hunted successfully that night. In comparison, only one of five collected from aggregations under shelter during midmorning had material in its stomach, and this was extensively digested (all had full intestines, however). Finally, all three that were collected from aggregations under shelter during late afternoon had completely empty guts, except for a few well-digested fragments posteriorly. Items in the 13 specimens containing identifiable material are listed in Table 14.

TABLE 14.—Food of *Holocentrus lacteoguttatum*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	13	36.3	36.30
2	Crab megalops	9	8.0	5.54
3	Gammaridean amphipods	8	5.1	3.14
4	Tanaids	6	3.7	1.71
5	Polychaetes	4	4.9	1.51
6	Caridean shrimps	3	1.9	0.44
7	Harpacticoid copepods	3	0.8	0.19
8	Echinoids	3	0.8	0.19
9	Sipunculid introverts	1	1.8	0.14
10	Prosobranch gastropods	1	1.0	0.08
11	Oxyrhynchid crabs	1	0.3	0.02
12	Calanoid copepods	1	0.3	0.02
13	Limpets	1	0.2	0.02
14	Ophiuroids	1	0.1	0.01
Also, crustacean fragments		13	28.1	28.10
	Unidentified fragments	4	6.7	2.06

CONCLUSION.—*Holocentrus lacteoguttatum* is a nocturnal predator that feeds primarily on benthic crustaceans, although some free-swimming forms close to the bottom are also taken.

Holotrachys lima (Valenciennes)

This fish is secreted far back in reef crevices during daylight. After dark, however, solitary individuals are widespread in exposed positions, swimming even closer to the reef than do the species of *Holocentrus,* discussed above. Unlike the others, which often swim over sand patches, this species stays over rock or coral. It did not display distinctive day or night color features, being at all times a solid rose-red.

Twenty specimens (91: 70-113 mm) were collected during day and night. Thirteen were active in exposed positions on the reef at night when speared, and the stomachs of eight contained prey, much of it fresh. Of the five taken after dark with empty stomachs, the entire gut was empty in three collected before midnight, indicating they had not yet hunted successfully that night; however, the gut was also empty in one speared just before dawn, indicating it had passed the entire night without feeding; the fifth individual with an empty stomach also was collected just before dawn, but its intestine was full, indicating that it probably had fed earlier during the night. Six of seven specimens collected from deep crevices during late morning had empty stomachs, and the extensively damaged material in the seventh individual probably had been ingested during the previous night. (Rotenone was used to collect this species during the day, a departure from the standard collecting method that was necessary because this secretive fish is only rarely seen in daylight.) Items in the 10 specimens containing identifiable material are listed in Table 15.

CONCLUSION.—*Holotrachys lima* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming forms close to the bottom also are taken.

Myripristis kuntee Cuvier

This is the smallest of the three species of *Myripristis* that are numerous on the nearshore Kona reefs. It remains secreted in small crevices

TABLE 15.—Food of *Holotrachys lima*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Caridean shrimps	6	31.5	18.90
2	Xanthid crabs	5	33.0	16.50
3	Crab megalops	2	7.0	1.40
4	Fish	1	3.5	0.35
5	Gammaridean amphipods	1	0.5	0.05
Also, crustacean fragments		5	24.5	12.25

and coral interstices during the day, but emerges and aggregates in the lower levels of the water column, above the reef, about 30 min after sunset. After remaining active during the night, it returns to its daytime shelter on the reef about 30 min before sunrise (Hobson, 1972, as *M. multiradiatus*). When this fish is under cover during the day its body is solid red, but when active in the water column after dark, its lower sides are silvery, affording countershading like that described for nocturnally active *M. leiognathus* in the Gulf of California (Hobson, 1968a). This nocturnal pattern was illustrated earlier (Hobson, 1972: Figure 6).

Thirty-nine specimens (120: 74-145 mm) were speared at different times of the day and night. All 20 that were collected either over the reef at night (later than 4 h after sunset), or from shelter sites within an hour of sunrise, had their guts full of food. In contrast, 13 of 14 collected from shelter sites during the afternoon and evening twilight had empty guts (3 had a few fragments posteriorly in their intestines), and the 14th had in its stomach only well-digested fragments. Of the remaining five, collected above the reef early during the night (within 1 h after last light), four had their guts completely empty, indicating they had not as yet hunted successfully at that early hour, but the fifth was full of fresh calanoid copepods of a species that was exceptionally numerous around our diving lights for about 45 min shortly after last light on that particular evening. Items in the 22 individuals that contained identifiable material are listed in Table 16.

CONCLUSION.—*Myripristis kuntee* is a nocturnal planktivore that takes mostly crab megalops and other crustacea.

Myripristis murdjan (Forskål)

This holocentrid is numerous in Kona, where during the day it aggregates in reef crevices and under coral overhangs, especially where there is shelter from prevailing seas (Figure 14). The twilight activity of this species has been described (Hobson, 1972, as *M. berndti*). About 30 min after sunset it emerges from its daytime shelter and aggregates in the water column above the reef, generally rising to levels higher than those attained by *M. kuntee* (see above). Immediately, there is a general movement offshore. It remains uncertain how far it swims offshore —perhaps it does not go much beyond the drop-off into deep water, which is a major feeding ground for diurnal planktivores (Hobson, 1972). The offshore move is obscured by the circumstance that at any given time during the night many individuals of this species are swimming over the inshore reefs. Nevertheless, there are consistently fewer of them over inshore reefs on dark nights than on moonlit nights. Gosline (1965) also noted offshore migrations at night by species of *Myripristis* in Hawaii. About 40 min before sunrise this species begins to assemble above its diurnal shelter, and within 10 min all have taken cover for the coming day. This species shows essentially the same day-night difference in color patterns as *M. kuntee*, above.

Of 25 individuals (169: 139-270 mm) speared at different times of day and night, all 16 that were taken above the reef at night (later than 4 h after

TABLE 16.—Food of *Myripristis kuntee*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Crab megalops	19	25.2	21.76
2	Decapod shrimps	9	11.8	4.83
3	Calanoid copepods	9	8.0	3.27
4	Mysids	7	9.3	2.96
5	Polychaetes	4	4.8	0.87
6	Fish	3	4.6	0.63
7	Stomatopods	4	2.8	0.51
8	Gammaridean amphipods	7	0.9	0.29
9	Gnathiid isopod larvae	2	1.8	0.16
10	Ostracods	2	0.1	0.01
11	Tanaids	1	0.1	0.01
12	Invertebrate eggs	1	0.1	0.01
Also, crustacean fragments		14	27.8	17.69
	Unidentified fragments	3	2.7	0.37

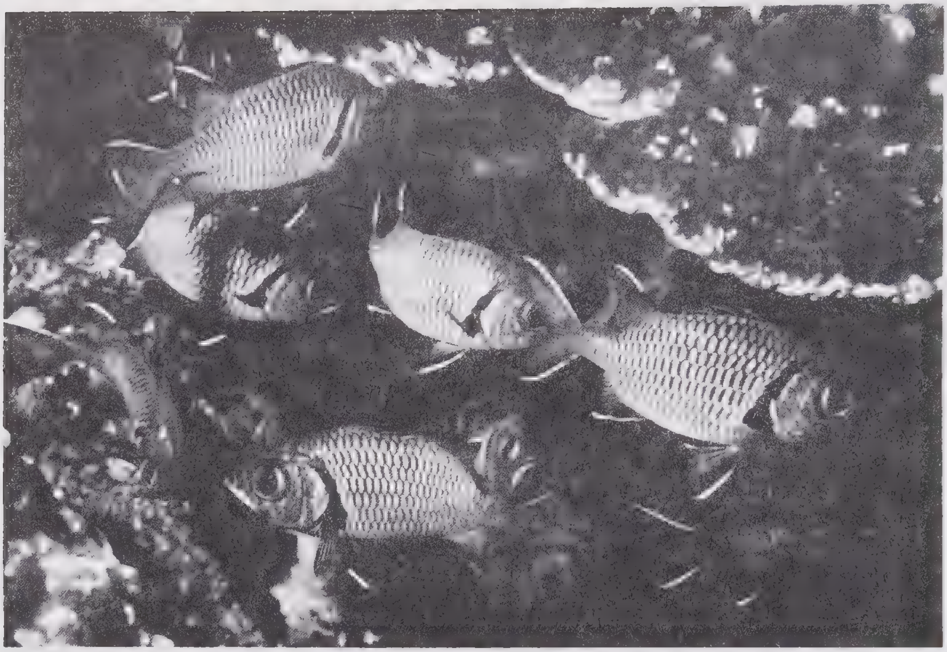


FIGURE 14.—*Myripristis murdjan*, a squirrelfish, aggregated under a coral ledge during the day.

sunset) contained food, whereas 8 of 9 that were collected from shelter sites during the afternoon were empty (the ninth specimen, collected during late afternoon, had only well-digested fragments in its stomach). Items in the 17 individuals containing identifiable material are listed in Table 17.

Hiatt and Strasburg (1960) found shrimp fragments in *M. murdjan* (reported as *M. berndti*) in the Marshall Islands, and suspected nocturnal habits, as did Randall (1955) for this species in the Gilbert Islands.

CONCLUSION.—*Myripristis murdjan* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

Myripristis amaenus (Castelnau)

This squirrelfish, which congregates during the day in large caves cut into reefs exposed to an open-sea swell, is very similar to the preceding, *M. murdjan*, but is less numerous in most Kona habitats. Its behavior during twilight was described earlier (Hobson, 1972, as *M. argyromas*).

TABLE 17.—Food of *Myripristis murdjan*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Crab megalops	16	53.5	50.35
2	Decapod shrimps	3	8.1	1.43
3	Mysids	3	6.5	1.15
4	Fish	2	2.0	0.24
5	Polychaetes	2	1.5	0.18
6	Stomatopods	2	0.9	0.11
7	Euphausiids	1	1.2	0.07
8	Cephalopods	1	1.2	0.07
9	Gammaridean amphipods	1	0.5	0.03
10	Prosobranch gastropods	1	0.3	0.02
11	Calanoid copepods	1	0.1	<0.01
12	Ostracods	1	0.1	<0.01
Also, crustacean fragments		8	14.5	6.82
	Unidentified fragments	4	9.6	2.26

Myripristis amaenus, like its congeners, emerges from its daytime retreats about 30 min after sunset, and at least many individuals move offshore, especially when there is no moonlight. *Myripristis amaenus* shows essentially the same day-night distinction in coloration that is described above for its congeners.

Of 19 individuals (176: 116-210 mm) speared at different times of day and night, all 14 collected above the reef at night (later than 4 h after sunset), or from shelter sites within 2 h after the species had returned to cover in the morning, contained food, whereas all 5 collected from shelter sites during late afternoon were empty. Items in the 14 individuals containing identifiable prey are listed in Table 18.

CONCLUSION.—*Myripristis amaenus* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

General Remarks on Squirrelfishes

Squirrelfishes are known throughout tropical seas to hunt prey after dark. For example, they have been thus described in the Marshall Islands (Hiatt and Strasburg, 1960), the Gulf of California (Hobson, 1965, 1968a), and the West Indies (Randall, 1967). Similar behavior has been noted in the Florida Keys by Starck and Davis (1966), who noted there were no distinctive nocturnal color features in tropical Atlantic holocentrids, such as are reported for all but two of the Hawaiian species above.

The two major categories noted above in the introduction to the squirrelfishes each represents a generally different mode of predation. All feed primarily on crustaceans, but whereas species of *Holocentrus* and *Holotrachys lima* capture their prey close to the sea floor, species of *Myripristis* hunt prey up in the water column.

BOTTOM FEEDERS.—The seven holocentrids in this category feed mostly on benthic forms, but also take some prey that are free-swimming at the base of the water column. Xanthid crabs comprised the major prey item for all species except the largest, *Holocentrus spinifera,* which contained a slightly larger volume of caridean shrimps. Xanthid crabs are ubiquitous benthic animals in all Kona inshore habitats, and are widely active in exposed positions after dark.

Of the seven bottom-feeding squirrelfishes, only three similar species, *Holocentrus diadema, H. lacteoguttatum,* and *H. xantherythrus,* hunt significantly over sand in addition to feeding on hard reef substrata; however, even these three do not range away from cover during this activity, which is limited to sand pockets on the reef and only the fringes of more extensive sandy areas. Nevertheless, it is probably because of this habit that these three have more varied diets than do the others. Hiatt and Strasburg (1960) reported that some of the holocentrids in the Marshall Islands forage on sandy bottoms, citing sand-dwelling gastropods as being prominent prey of *H. diadema* in that area.

The other four bottom feeders, *Holocentrus sammara, H. spinifera, H. tiere,* and *Holotrachys lima,* restrict their activity largely to hard substrata on the reef, and prey more heavily on caridean shrimps—especially on snapping shrimps. Some of the larger individuals of *Holocentrus sammara* and *H. spinifera* capture the caridean *Saron marmoratus*; although individuals of this shrimp exceeding a length of 30 mm are numerous

TABLE 18.—Food of *Myripristis amaenus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Crab megalops	14	75.1	75.10
2	Decapod shrimps	4	9.3	2.66
3	Fish	3	2.9	0.62
4	Cephalopods	1	1.4	0.10
5	Mysids	4	0.3	0.09
6	Prosobranch gastropods	2	0.4	0.06
7	Polychaetes	1	0.4	0.03
8	Gammaridean amphipods	1	0.2	0.01
9	Calanoid copepods	1	0.1	<0.01
10	Stomatopods	1	0.1	<0.01
11	Isopods	1	0.1	<0.01
Also, crustacean fragments		8	9.7	5.54

in exposed positions on the reef after dark, most are too large to serve as prey for all but the biggest squirrelfishes.

WATER-COLUMN FEEDERS.—These are the species of *Myripristis,* all of which are primarily planktivores. This habit is reflected in their sharply upturned mouths, a feature well known as adaptive to feeding on plankton (e.g. Rosenblatt, 1967). Based on the food-habit data, crab megalops are the major prey of all three species reported here.

Earlier (Hobson, 1965, 1968a), I reported that *M. leiognathus* in the Gulf of California feeds in the water column after dark on planktonic crustaceans, including crab larvae. Similarly, Randall (1967) reported that *M. jacobus* in the tropical Atlantic feeds at night primarily on planktonic organisms, especially crustacean larvae, and Collette and Talbot (1972) noted that this species feeds at least 3 m above the reef. Probably similar habits are universal in species of *Myripristis.*

ORDER GASTEROSTEIFORMES

Family Aulostomidae: trumpetfishes

Aulostomus chinensis **(Linnaeus)—*nunu***

This distinctive, solitary fish (Figure 15) is numerous on Kona reefs, where it attains the length of at least 700 mm. It exhibits three basic color forms: plain reddish brown, brown with light striping and other marks, and plain yellow. Several trumpetfish recognized as individuals were seen repeatedly in the same areas throughout the study, and none changed coloration during this time. The habitat of this species is in water deeper than about 5 m close to coral or irregular rocky substrata that offer many ledges and crevices.

I observed no difference in the behavior of this fish between day and night. At all hours it moves slowly, close to cover, propelling its long, cylindrical, rod-straight body mainly by undulating its soft dorsal and anal fins, which are set far back near the tail. The trumpetfish is a stalking predator, and on a few scattered occasions I saw it

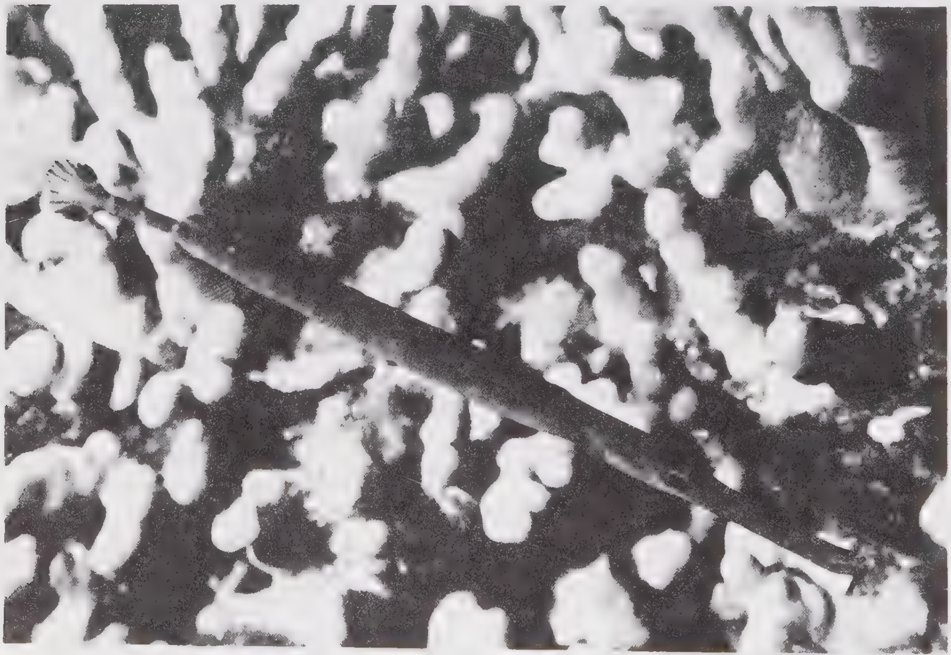


FIGURE 15.—*Aulostomus chinensis,* the trumpetfish, a stalking predator.

capture prey during daylight. After gaining a position close to its quarry, the attack is consummated with a short dart forward, the victim being literally sucked in with a sudden expansion of its tubular snout. Hiatt and Strasburg (1960) did not observe feeding, but speculated that this species in the Marshall Islands probes with its long snout in shallow holes and interstices of the reef and captures prey there by rapidly dilating its mouth. They found a small atherinid fish in the gut on one specimen. Sometimes trumpetfish accompany schools of grazing surgeonfishes—usually mixed groups of *Acanthurus sandvicensis* and *A. nigroris,* which frequently move across the reef. At these times, small organisms probably are driven out from algal cover by the grazing herbivores and become available as prey to the trumpetfish. Occasionally, the trumpetfish swims close beside large herbivores, especially parrotfishes, apparently using these large fishes as shields behind which to get close to prey not threatened by the herbivore.

Although 52 individuals (410: 220-621 mm) were speared at different times of day and night, no pattern was evident in the condition of the gut contents from specimens taken at these different times. Of 27 that contained food in their stomachs, 18 had captured fishes (mean percent of diet volume: 63; ranking index: 42), and 11 had taken caridean shrimps (mean percent of diet volume: 37; ranking index: 15.07).

It probably is significant that, with only two exceptions, those sampled had preyed on either fishes or shrimps—not both. The data cannot relate this selectivity to day or night activity or to size of predator. The 16 individuals that had preyed exclusively on fishes were within exactly the same size range (241-528 mm) as the 9 individuals that had preyed exclusively on shrimps. Furthermore, the mean sizes of the two groups differed only slightly—401 mm for the fish eaters, 396 mm for the shrimp eaters. The two individuals that had taken both fishes and shrimps were 241 and 337 mm long.

Aulostomus chinensis takes relatively large prey: the 15 fish items (representing among others *Apogon snyderi, Acanthurus nigrofuscus, Canthigaster* sp., and a labrid) that could be measured accurately had a mean standard length of 58 mm (range 25-88 mm) whereas the 11 shrimps that could be measured accurately had a mean total length of 55 mm (range 13-110 mm). Ten of the 11 shrimps were *Saron marmoratus,* the only shrimp this large that was numerous in exposed locations on the reef. Although this shrimp occupies exposed positions only at night, I have no evidence that it is taken by *Aulostomus chinensis* in greater numbers after dark.

Because the trumpetfish has an especially long, attenuated body, and because it takes relatively large prey, individuals that have recently ingested a meal often can be recognized by their distended bellies. Such individuals were occasionally seen during all periods of day and night, but most often during, or shortly after, twilight. Consistent with this, all three specimens that contained fresh prey (little or no damage by digestion) were collected during late twilight: in two of these instances (one in the morning, one in the evening) the prey were fishes; in the other instance (evening), the prey was a shrimp, *S. marmoratus.* Beyond this, the gut contents were of little help in establishing a pattern to feeding times; nor did the incidence of individuals with empty stomachs indicate a pattern, for they were collected during all periods of day and night.

CONCLUSION.—*Aulostomus chinensis* stalks prey, mostly fishes and caridean shrimps, most successfully during twilight, but also during the day and perhaps also at night.

General Remarks on Trumpetfishes

The activity of *Aulostomus chinensis* in Kona seems to be typical of the genus in other seas. Randall (1967) reported only fishes and caridean shrimps in 79 *A. maculatus* from the West Indies, and also remarked on the large size of these prey, as well as the way this trumpetfish sucks them into its mouth by expanding its tubular snout. Randall often observed *A. maculatus* hovering vertically in the water over small fishes and several times darting down on them (I did not see *A. chinensis* feed this way). Collette and Talbot (1972) judged *A. maculatus* in the Virgin Islands to be primarily crepuscular. They were uncertain about its nocturnal activity, but judged one they saw in a gorgonian at 2330 h to be quiescent. Eibl-Eibesfeldt (1955) described the way trumpetfish in the Indian Ocean use other fishes as cover behind which to approach small prey, and this was also reported by Collette and Talbot (1972) from the Virgin Islands.

Family Fistulariidae: cornetfishes

Fistularia petimba Lacépède

The cornetfish (see Hobson, 1968a: Figure 9) looks much like the trumpetfish, but grows considerably larger, many being over 1 m long. It is a pale-green fish with light-blue markings, and under certain circumstances instantaneously displays a series of broad bands along its body. Earlier I (Hobson, 1968a) reported that this species in the Gulf of California displays these bands when poised to strike prey. In Kona, the bands appear in similar circumstances and also in situations that suggest the fish might feel threatened, as when it is approached underwater by a human—especially a human carrying a diving light at night. *Fistularia petimba* frequently swims in loosely spaced groups of several individuals, generally in exposed shallowwater locations over the reef top.

Occasionally, *F. petimba* was seen in Kona stalking its prey during daylight, as observed in the Gulf of California (Hobson, 1968a). It does not move suddenly until within a few centimeters of its prey. When positioned for attack, it often draws its midsection into a modified "s" (as viewed from above), then darts forward for the capture. *Fistularia petimba* is more agile than *A. chinensis,* and undulating body movements not seen in the latter are regularly used to provide greater thrust in attacks and accelerated swimming. In the Gulf of California, I saw *F. petimba* use other fish as shields behind which to approach prey, as described above for *A. chinensis,* but did not see this in Kona. The behavior of *F. petima* was not seen to differ between day and night.

The 10 specimens (673: 363-1,069 mm), although collected during both day and night, were too few to provide much evidence on feeding times; however, of the 2 with empty guts, 1 was collected during late afternoon, and the other just before first morning light, indicating that these 2 had not fed during the preceding day and night, respectively. Only two specimens contained fresh prey, and both were collected shortly after twilight —one after evening twilight, the other after morning twilight. Though limited, these data suggest crepuscular feeding. Although prey in the other six specimens were in stages of digestion not inconsistent with predominantly crepuscular feeding, they clearly showed that prey are also taken at other times. All eight individuals with material in their stomachs had fed on fishes exclusively; only two prey could be identified to species, one a 70-mm cardinalfish, *Apogon snyderi,* the other a 52-mm damselfish, *Abudefduf imparipennis.* Both of these prey could have been captured close to reef crevices during the day.

Thus, *F. petimba* in Kona, as in the Gulf of California (Hobson, 1968a), was found to prey only on fishes. Hiatt and Strasburg (1960) also reported this species in the Marshall Islands to be exclusively piscivorous. My data suggest that *F. petimba* takes somewhat smaller prey than does *A. chinensis* of comparable length, as might be expected in view of the deeper body and snout of the latter. The mean length of the seven *F. petimba* containing measurable prey was 593 mm (range: 363-795 mm). The 11 measurable prey in these individuals had a mean length of 32 mm (range: 8-70). Comparable data for *A. chinensis* are given above.

CONCLUSION.—*Fistularia petimba* stalks fishes most successfully during twilight, but also during the day and perhaps at night.

General Remarks on Cornetfishes

The exclusively piscivorous habits of *Fistularia petimba* are paralleled by the similar diet of *F. tabacaria* in the tropical Atlantic (Randall, 1967). Suyehiro (1942) claimed that *F. petimba* feeds on tiny floating organisms by using its snout like a pipette, but I join Hiatt and Strasburg (1960) and Randall (1967) in contesting this opinion of the size of its prey. Starck and Davis (1966) found *F. tabacaria* to be more numerous on Florida reefs at night than during the day, but did not speculate that this reflected differences in feeding behavior.

ORDER SCORPAENIFORMES

Family Scorpaenidae: scorpionfishes

Pterois sphex Jordan and Evermann — lionfish, *nohu pinao*

The lionfish is a sluggish, solitary species that usually rests motionless on the reef, yet draws attention by its spectacular appearance (Figure 16). Perhaps because its fin spines carry a potent toxin, this fish makes little effort to evade a human collector. It is not numerous in Kona, and

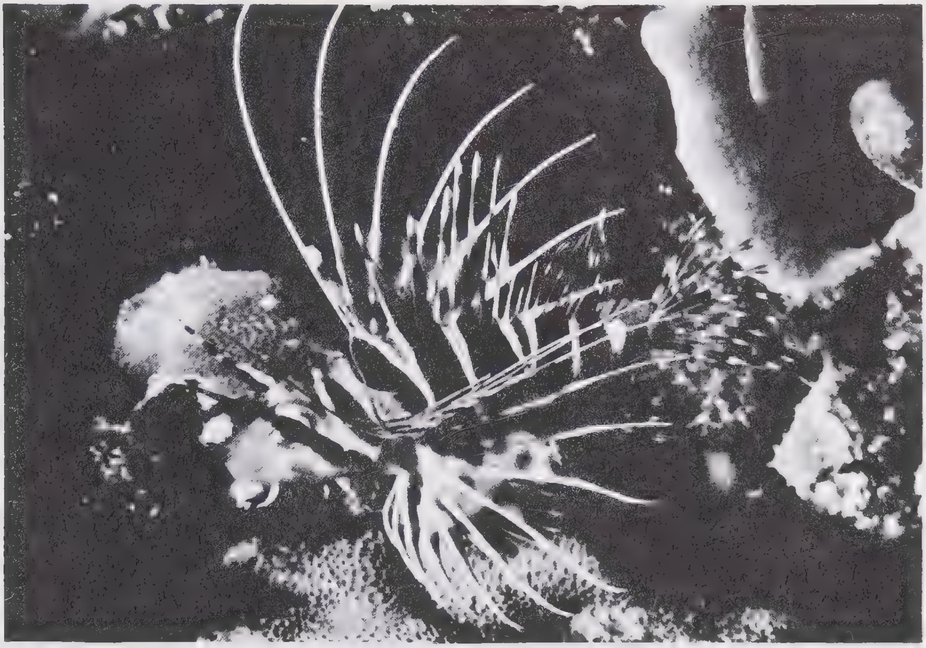


FIGURE 16.—*Pterois sphex*, a lionfish, swimming close to the reef at night.

occurs in visible locations on the reef most often after dark—though never far from shelter.

Fourteen specimens (83: 58-121 mm) were speared during day and night. Of nine that were collected during the afternoon or evening twilight, the guts in six were empty, and three had only well-digested crustacean fragments in their stomachs. On the other hand, all five specimens collected at night (more than 2 h after sunset) contained relatively fresh prey in their stomachs.

All eight specimens that contained food had fed on crustaceans exclusively. Caridean shrimps, which occurred in six, were the major food item (mean percent of diet volume: 56.3; ranking index: 42.19). Other food items were: xanthid crabs in three (mean percent of diet volume: 13.8; ranking index: 5.16) and pagurid crabs in one (mean percent of diet volume: 0.6; ranking index: 0.08). Five individuals contained unidentified crustacean fragments (mean percent of diet volume: 29.4; ranking index: 18.36).

CONCLUSION.—*Pterois sphex* is a nocturnal predator that takes benthic crustaceans, especially caridean shrimps.

Scorpaena coniorta (Jenkins)

Although this small species is the most numerous scorpaenid on Kona reefs, the casual observer will encounter it only at night. During the day individuals more than about 50 mm long are deep in reef crevices, whereas many smaller individuals are motionless among the branches of the coral *Pocillopora meandrina* (Figure 17). After nightfall, many of these fish occur in exposed positions: the larger individuals are spread widely across the reef, resting immobile on rock or coral, whereas the smaller ones are perched motionless on the sea floor close by the same coral heads that shelter them during the day. However, at any given time of night some of these fish are among the coral branches, just as in daylight.

Thirty-four specimens (46: 36-67 mm) were collected during various times of day and night. Of 12 that were taken during afternoon or early evening, most from among coral branches, only 1 had food in its gut (3 had a few fragments posteriorly in their intestine). The one containing food, taken from a coral head, had in its stomach a crab that, based on damage by digestion, probably had been

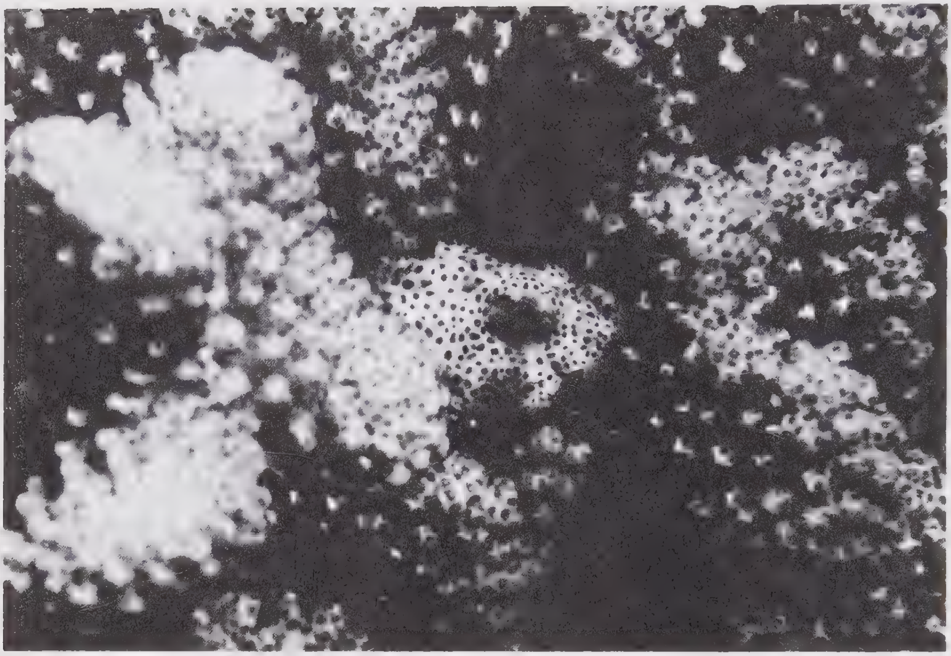


FIGURE 17.—*Scorpaena coniorta,* a scorpionfish, nestled among coral branches during the day.

captured during the day. In comparison, 14 of 22 individuals collected at night, between 3 h after sunset and first morning light, had food in their stomachs. Brachyuran crabs, almost all of them xanthids, occurred in 7 of the 15 individuals that contained identifiable items (mean percent of diet volume: 39; ranking index: 18.2). Caridean shrimps occurred in six (mean percent of diet volume: 28.3; ranking index: 11.33), and fishes in one (mean percent of diet volume: 6.7; ranking index: 0.45). Unidentified crustacean fragments occurred in six (mean percent of diet volume: 26; ranking index: 10.4). Many of the xanthids and carideans found in specimens less than 50 mm long are forms that cooccur with these fish among the coral branches.

CONCLUSION.—*Scorpaena coniorta* is a nocturnal predator that takes benthic crustaceans, mostly xanthid crabs and caridean shrimps. Some prey are also captured during the day.

Scorpaenopsis cacopsis Jenkins—*nohu 'omakaha*

This species, the largest Hawaiian scorpaenid, grows to over 50 cm long (Gosline and Brock, 1960). I observed no overt difference in its behavior between day and night as it was seen resting immobile on the reef at all hours, often fully exposed. Despite its large size and frequent disdain for cover, this fish remains virtually unseen, owing to body hues and texture that render it much like the reef on which it rests. It was not seen feeding, but its morphology and behavior suggest that it lunges forward to attack prey that have strayed within range, and sucks them in with a sudden expansion of its cavernous mouth.

Of the five specimens (256: 73-375 mm) examined, three had prey in their stomachs: one, taken within 1 h after sunrise, contained a fresh fish, *Pomacentrus jenkinsi* (104 mm); a second taken at night, 4 h after sunset, contained a relatively fresh octopus; and the third, taken late in the afternoon, contained fish fragments. The other two, both empty, were collected during morning twilight.

CONCLUSION.—*Scorpaenopsis cacopsis* attacks fishes and motile invertebrates during the day. Its nocturnal activity remains uncertain.

General Remarks on Scorpionfishes

Scorpionfishes on tropical reefs are widely described as predators that rest on the bottom, and because they resemble their surroundings they remain unseen by small prey that swim within striking range (Longley and Hildebrand, 1941; Hiatt and Strasburg, 1960; Starck and Davis, 1966; Randall, 1967). This behavior is descriptive of some scorpaenids, but probably is overdrawn as a generalization encompassing the entire family. Such a tactic is adaptive to daylight, and is used by *Scorpaenopsis cacopsis* in Hawaii (the one fish identified as prey of this predator, a damselfish, is strictly a diurnal species that is not active over the reef at night). Significantly, the fishes that have been reported by other investigators as prey of scorpaenids on tropical reefs similarly imply diurnal predations: blennies (Longley and Hildebrand, 1941); a wrasse and a parrotfish (Hiatt and Strasburg, 1960); and an angelfish, a surgeonfish, a sardine, a sea horse, and a conger eel (Randall, 1967). With perhaps the lone exception of the conger eel, these are fishes that swim close to the reef during daylight, and at that time would be vulnerable to the ambushing tactic of scorpaenids; however, they would not be readily available after dark when most of them rest under cover on the reef or, in the case of the sardine, swim away from the reef. Conspicuously absent among the reported prey are the many species of comparable size that are numerous close above the reef at night, including apogonids and holocentrids. One can readily see how camouflage and ambush would be especially suited to daylight, but less significant after dark. Randall (1967), basing his generalization on the West Indian situation, characterized the scorpaenids as diurnal. In Hawaii, most species are predominantly nocturnal. In addition to *Pterois sphex* and *Scorpaena coniorta,* which prey largely on benthic crustaceans, as described above, other members of the family that appear on the reef in greater numbers at night include *Dendrochirus brachypterus, Scorpaenodes parvipinnis,* and *Scorpaena ballieui.* Among feeding scorpaenids, camouflage does not seem to play the important role at night that it does during the day. When these predators are abroad after dark they often contrast markedly with their surroundings. Although fishes do not seem to be significant prey at night, the behavior of these nocturnal scorpaenids indicates that their tactic remains a short lunge from a resting position to capture prey that have inadvertently come within range.

ORDER PERCIFORMES

Family Serranidae: sea basses

Sea basses are prominent on most tropical reefs, but the family has no representatives native to shallow Hawaiian reefs (Gosline and Brock, 1960). Nevertheless, the widespread Indo-Pacific serranid *Cephalopholis argus* has been introduced into Hawaii from the Society Islands, the first time in 1956, and has since become well established in Kona.

Cephalopholis argus Bloch and Schneider

This solitary fish, numerous on Kona reefs, swims close among overhanging ledges and crevices during the day, but is seen less often at night. Because it generally is wary of humans, lack of nocturnal observations could mean that it avoided our diving lights at night.

Although 6 of 10 specimens (319: 232-520 mm) speared at various times of day were empty, no temporal pattern is recognized, as the 6 were taken from early morning to late afternoon. All four that contained food, also taken at various times during the day (on four different occasions over 3 mo), had fed exclusively on fishes. One, taken during midmorning, contained, because of digestion, what was recognizable only as a fish (125 mm). The other three—one collected during midday, and two late in the afternoon—each contained a single moderately digested squirrelfish, *Holocentrus xantherythrus* (80, 110, and 130 mm, respectively). *Holocentrus xantherythrus* congregates under ledges during the day in areas where *C. argus* is active (see the species account for *H. xantherythrus* above), and thus is available as prey for the sea bass at this time. *Cephalopholis argus* has been reported to feed on shrimps as well as fishes in the Marshall Islands (Hiatt and Strasburg, 1960) and on shrimps in the Gilbert Islands (Randall, 1955). In a sample of 98 specimens from Tahiti, Randall and Brock (1960) found that 77.5% contained fishes, whereas 22.5% contained crustaceans (shrimps and crabs).

CONCLUSION.—*Cephalopholis argus* preys on fishes among reef crevices during the day. Its nocturnal habits remain uncertain.

General Remarks on Sea Basses

Diurnal piscivorous habits were reported in *Mycteroperca rosacea* in the Gulf of California, with peaks during twilight (Hobson, 1965, 1968a). On the other hand, nocturnal habits were noted in *Alphestes multiguttatus* and *Rypticus bicolor* (the latter is often placed in a separate family, the Grammistidae), both of which prey chiefly on benthic crustaceans (Hobson, 1965, 1968a). In the same reports, a fourth sea bass, *Epinephelus labriformis,* was reported to feed by both day and night, chiefly on fishes in daylight and on benthic crustaceans after dark. These data suggest that fishes may be the major prey of sea basses in daylight with crustaceans predominating after dark, a generalization consistent with the limited observations on *Cephalopholis argus* in Kona.

Starck and Davis (1966) noted that serranids of the genera *Epinephelus, Mycteroperca,* and *Petrometopon* behave similarly day and night in the Florida Keys, with probable feeding peaks around sunrise and sunset. Longley and Hildebrand (1941) reported that *Epinephelus morio* feeds during both day and night in the Dry Tortugas, Fla., and Randall (1967) noted that larger serranids in the West Indies feed both day and night, with greatest activity at dawn and dusk. Collette and Talbot (1972), on the other hand, reported *E. guttatus* in the Virgin Islands to be active by day and apparently asleep at night. They also found *E. fulvus* and *E. cruentatus* active in daylight and suspected that these sea basses rest at night. Randall (1967) considered the smaller serranids, in general, to be primarily diurnal. In Florida, Starck and Davis (1966) regarded certain small serranids of such genera as *Diplectrum, Hypoplectrus,* and *Serranus* to be active by day and inactive by night. None of these authors attempted to relate time of activity with kinds of prey.

Family Kuhliidae: aholeholes

Kuhlia sandvicensis (Steindachner)—*aholehole*

This predator occurs in only a few locations within the Kona study area, and there just sparsely, compared to its large numbers elsewhere in Hawaiian nearshore waters. Juveniles and young adults live in tide pools or in schools close to shore (Gosline and Brock, 1960), but the larger adults congregate during the day under low ledges and boulders, usually in water less than 5 m deep farther from shore. They emerge from shelter at nightfall, and the few observed after dark during this study were solitary in the water column over the reef. Gosline and Brock (1960) noted that the adults, at least, are nocturnal, a conclusion consistent with the large eyes of the species.

Of the 13 specimens (164: 132-202 mm) collected, 8 speared during midmorning from under rocky cover contained in their stomachs extensively digested crustacean fragments (including crab megalops), 1 taken under a rock at noon contained only well-digested material scattered through its intestine, and 4 speared under rocks late in the afternoon were empty.

CONCLUSION.—*Kuhlia sandvicensis* is a nocturnal predator that feeds on free-swimming crustaceans.

Family Priacanthidae: bigeyes

Priacanthus cruentatus (Lacépède)—bigeye, *aweoweo*

This priacanthid (Figure 18) is numerous in Kona, where it takes shelter under rocks or coral during the day, often in groups, and is active in the open at night. After emerging from shelter at nightfall, many individuals assemble in schools high in the water column and then migrate offshore. These do not return inshore until about 40 min before sunrise, but a lesser number of other individuals, mostly solitary or in small groups, remain over the inshore reefs throughout the night. All of these fish return to their daytime shelter by 30 min before sunrise, at least many of them to specific home caves (Hobson, 1972).

Forty specimens (173: 115-255 mm) were collected during day and night. All 17 that were speared during morning twilight (shortly after they had reappeared near their diurnal shelter, but before they had taken cover) had relatively fresh prey in their stomachs. Four others were collected from under cover during late morning, and although all had full stomachs, with many items identifiable, digestion was advanced, and most of the material was damaged beyond recognition. The other 19 were collected from caves late in the afternoon, and although only 4 of these had empty stomachs, the material in the other 15 was reduced to unidentified fragments. Items in the 21 specimens containing identifiable material are listed in Table 19.

Hiatt and Strasburg (1960) acknowledged that species of *Priacanthus* generally are thought to be nocturnal, but contested this opinion as far as *P.*

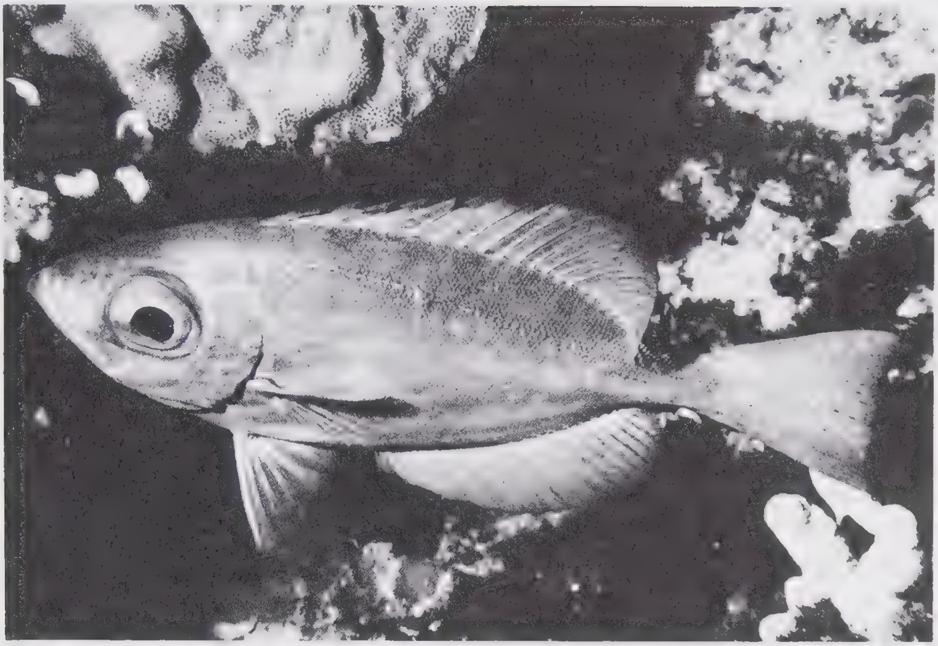


FIGURE 18.—*Priacanthus cruentatus*, a bigeye, showing the plain red coloration typical of this species when among the coral during the day.

cruentatus in the Marshall Islands is concerned. Although conceding the possibility of some nocturnal feeding, they believed that this species captures octopods, a major food there, in reef crevices and caves during the day. This conclusion was heavily influenced by finding food in the stomachs of this priacanthid during the day, but none in stomachs of the nocturnally active holocentrids. As noted above, I found a similar difference between *P. cruentatus* and holocentrids in Kona, but attribute this to the priacanthid retaining food in its stomach longer during digestion than do holocentrids.

Longley and Hildebrand (1941) noted that this circumtropical species feeds chiefly at night in Florida, a conclusion with which Starck and Davis (1966) concurred. In the West Indies, Randall (1967) was of the same opinion, but he also felt that the condition of prey in some specimens indicated diurnal feeding as well; Randall noted that *P. cruentatus* preys mostly on the larger animals in the plankton. Collette and Talbot (1972) concluded that in the Virgin Islands this is a crepuscular species that continues to feed in caves and under ledges during daytime.

Gosline (1965) reported that *P. cruentatus* in

TABLE 19.—Food of *Priacanthus cruentatus*.

Rank	Items	No. fish with this item (n = 21)	Mean percent of diet volume	Ranking index
1	Crab megalops	17	32.3	26.15
2	Cephalopods	8	20.4	7.77
3	Fish	6	11.2	3.20
4	Decapod shrimps	5	3.6	0.86
5	Adult crabs	2	7.6	0.72
6	Mysids	1	0.4	0.02
7	Stomatopods	1	0.1	0.01
Also, crustacean fragments		11	13.4	7.02
	Unidentified fragments	8	11.0	4.19

Hawaii migrates offshore at night. In Florida, however, Starck and Davis (1966) noted only that it is active at night in the same areas where it is sheltered in daylight; they illustrated this species with a mottled color pattern, which they believed to be its nocturnal coloration. The same mottled pattern occurs regularly at night in Kona when the fish is held in the beam of a diving light, and I believe it is a response to the light, rather than a nocturnal coloration—especially because the pattern is intensified upon moving the light progressively closer to the fish. In the absence of a diving light at night, this species is either plain red (as it usually is in daylight), or, more often with individuals in mid-water, overall pale-silver (occasionally this pale-silver coloration is displayed under cover during the day). The blotched pattern is the red and silver hues in combination.

CONCLUSION.—*Priacanthus cruentatus* is a nocturnal predator that feeds on free-swimming organisms, mostly crustaceans and cephalopods.

Family Apogonidae: cardinalfishes

Apogon erythrinus Snyder

After dark, this small solitary cardinalfish is numerous close to basalt reefs in water less than 6 m deep, usually in small sand and cobble pockets. The smaller ones are largely transparent, and transparency remains a characteristic of even the largest individuals, despite an increased pinkish hue (Figure 19). During the day *A. erythrinus* remains out of sight, secreted deep in reef crevices.

Of 14 individuals (36: 22-42 mm) examined, 4 that had been collected together from a deep crevice 4 h after sunrise were empty (rotenone was used to collect these 4, a departure from the standard collecting method necessary here because the species was never visible during the day). The other 10 specimens were speared from among those active in exposed locations on the reef at night (more than 4 h after sunset), and although 2 were empty, the other 8 contained prey in their stomachs.

All eight with material in their stomachs contained crustaceans exclusively. Xanthid crabs

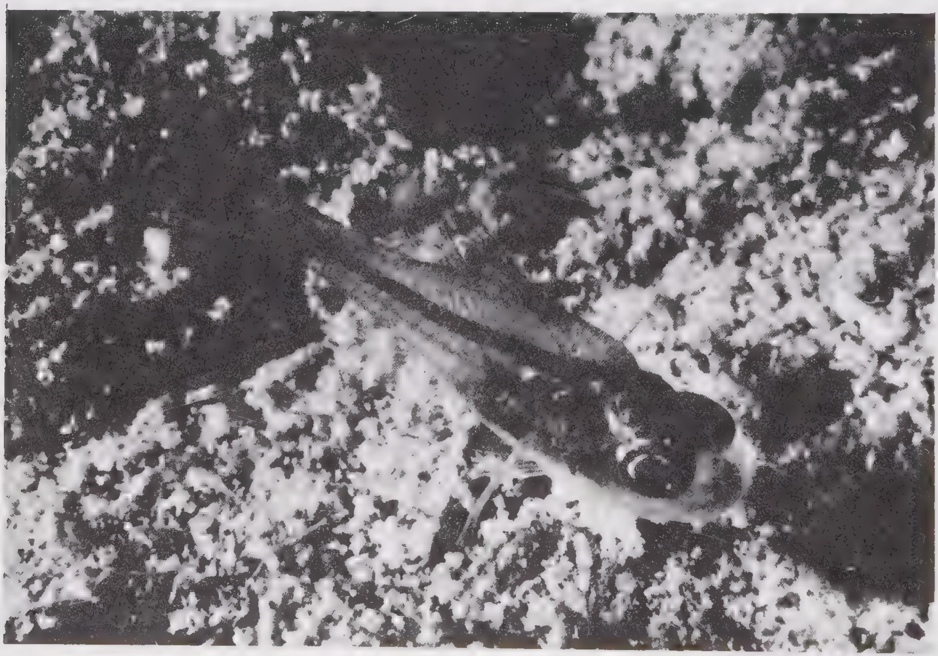


FIGURE 19.—*Apogon erythrinus*, a cardinalfish, showing the transparency typical of this species as it swims close to the reef at night.

were the major item, occurring in five individuals (mean percent of diet volume: 50; ranking index: 31.25). Most of these xanthids were in the megalops stage, except that their abdomens were reflected under their carapaces. The only other identifiable prey, occurring in three specimens, were gammaridean amphipods (mean percent of diet volume: 20; ranking index: 7.5). Four contained unidentified crustacean fragments (mean percent of diet volume: 30; ranking index: 15).

CONCLUSION.—*Apogon erythrinus* is a nocturnal predator that takes mostly benthic crustaceans.

Apogon menesemus Jenkins—*'upapalu*

This species and the very similar *A. snyderi* (below) are the largest and most abundant apogonids in Hawaii (Gosline and Brock, 1960), and they were the apogonids seen most often during the present study. During the day, *A. menesemus* hovers quietly in the deep shadows of reef crevices, but during late evening twilight emerges into the open. Throughout the night solitary individuals hover about 1 m above the coral. On several occasions after dark this cardinalfish struck at the silver barb on my otherwise dark spear: sometimes when this happened the spear was faintly illuminated by my partner's diving light, but other times moonlight provided the only illumination. At first morning light *A. menesemus* moves close to cover on the reef, and during morning twilight returns to its daytime shelter. When under cover during the day its coloration is relatively featureless, but when in the open at night distinctive fin markings appear (Figure 20a and b).

Fifty-nine specimens (114: 90-134 mm) were collected during day and night. Of the 14 that were speared from reef caves during late afternoon, only 2 had food in their stomachs—one contained an extensively digested piece of meat that probably was the remains of prey captured the previous night, whereas the other contained a relatively fresh xanthid crab that appeared to have been captured earlier that day. In comparison, 25 of 40 specimens collected at night, between 3 h after sunset and first morning light, had food in their stomachs—much of it fresh. Finally, of five specimens collected from caves during early morning, within 3 h after sunrise, four had food in their stomachs. Items in the 31 individuals containing identifiable material are listed in Table 20.

Two individuals that each contained just a single xanthid crab are the only ones that indicated exclusively benthic feeding; significantly, one of these was the lone individual, noted above, that appeared to have fed while under cover during the day. The other, collected in the open just 3 h after sunset, may also have taken its prey before leaving shelter in the evening. *A. menesemus* takes mostly free-swimming prey, presumably at its regular nocturnal station above the reef. Nevertheless, judging from the sand mixed with food in one individual collected at midnight, some prey are taken from the sea floor after dark.

CONCLUSION.—*Apogon menesemus* is a nocturnal predator that feeds mostly on free-swimming crustaceans.

Apogon snyderi Jordan and Evermann—*'upapalu*

This cardinalfish cooccurs with the very similar *A. menesemus,* above, but the two species remain at least partially segregated. During the day both species occupy the same caves, but *A. snyderi* is not so deep in the shadows and, in fact, frequently hovers at the entrances. Like *A. menesemus, A. snyderi* emerges into the open during evening twilight, but during the night stays closer to the sea floor; furthermore, whereas *A. menesemus* mostly remains over coral, *A. snyderi* tends to move over the sand patches within the reef and in the fringes of the more extensive sand areas adjacent to the reef. On several occasions at night, *A. snyderi* struck at the silver barb on my spear, just as described above for *A. menesemus. Apogon snyderi* does not have prominent nocturnal color features, as does *A. menesemus*. When over sand at night its body has a highly reflective bluish cast, also shown to a lesser extent by *A. menesemus,* but which is largely lost by both species soon after they move over coral or rocks.

Thirty specimens (96: 82-130 mm) were speared during day and night. All 3 that were taken from caves during the afternoon had empty stomachs, whereas of 24 collected in the open at night, between 2 h after sunset and first morning light, 22 had food in their stomachs. The remaining three were collected from caves during the 4 h after sunrise, and while two of these had food in their stomachs, the third was empty. Items in the 24 individuals containing identifiable material are listed in Table 21.

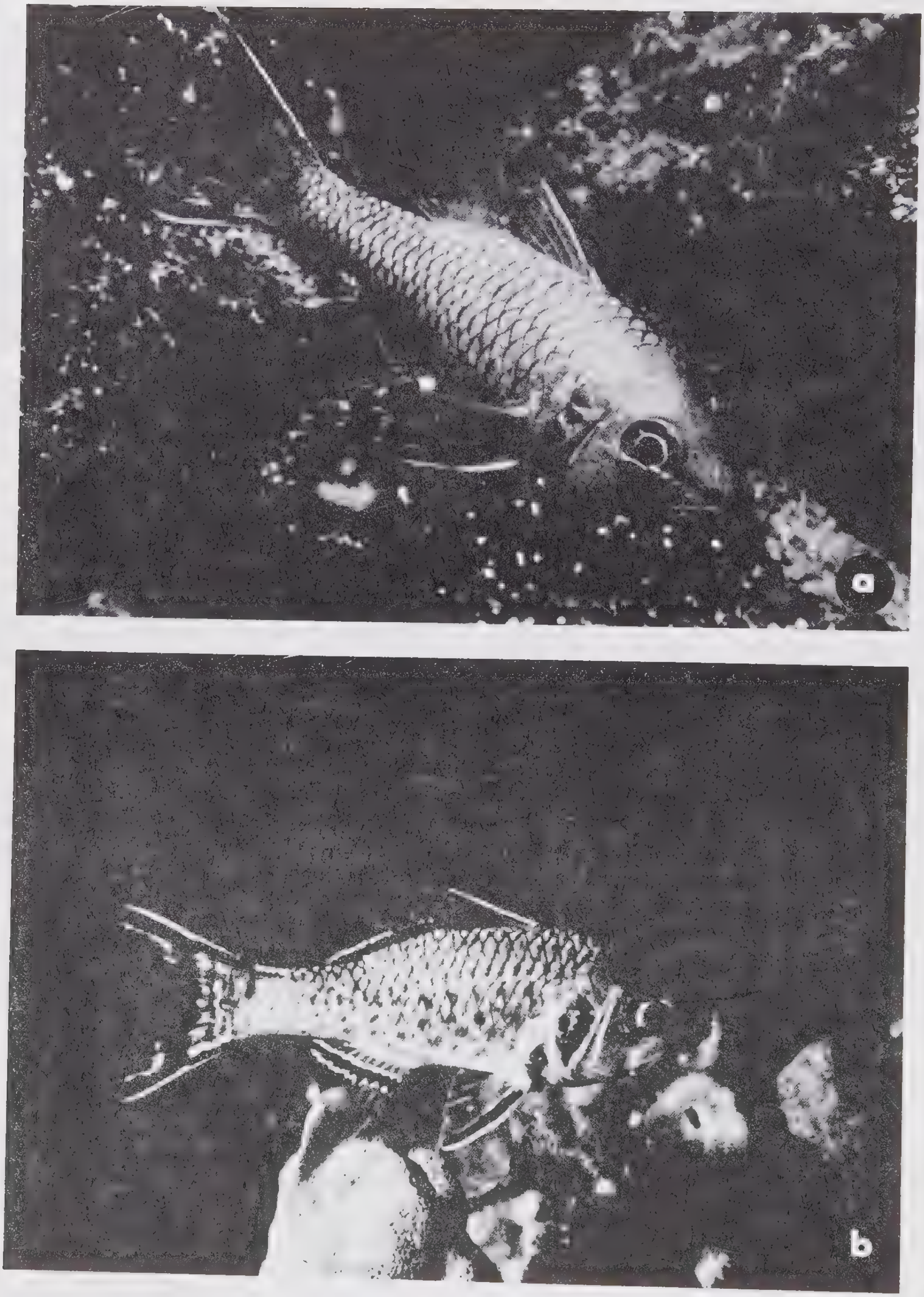


FIGURE 20.—*Apogon menesemus*, a cardinalfish: a, showing its diurnal coloration under a ledge during the day; b, showing its nocturnal coloration as it swims above the reef at night.

TABLE 20.—Food of *Apogon menesemus*.

Rank	Items	No. fish with this item (n = 31)	Mean percent of diet volume	Ranking index
1	Crab megalops	10	17.6	5.68
2	Decapod shrimps	11	15.7	5.57
3	Xanthid crabs	2	6.9	0.45
4	Mysids	3	2.9	0.28
5	Fish	1	2.0	0.07
6	Gammaridean amphipods	1	0.8	0.03
7	Isopods	1	0.2	<0.01
8	Copepods	2	0.1	<0.01
9	Gastropod larvae, echinospira	1	0.1	<0.01
Also,	crustacean fragments	20	40.0	25.81
	Unidentified fragments	6	13.7	2.65

TABLE 21.—Food of *Apogon snyderi*.

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Decapod shrimps	12	34.3	17.15
2	Xanthid crabs	6	14.6	3.65
3	Crab megalops	4	7.5	1.25
4	Fish	2	5.6	0.47
5	Mysids	2	2.1	0.18
6	Hippid crabs	1	4.2	0.18
7	Polychaetes	1	2.9	0.12
8	Copepods	1	1.3	0.05
9	Gammaridean amphipods	1	1.3	0.05
10	Sipunculid introverts	1	0.2	<0.01
Also,	crustacean fragments	12	25.4	12.70
	Unidentified fragments	1	0.6	0.03

The diet of *A. snyderi,* compared with that of *A. menesemus,* includes a greater proportion of benthic organisms, especially forms from sandy bottom, like hippid crabs. Nevertheless, many of the prey of *A. snyderi* are free-swimming forms that may or may not have been in the water column when captured. The major item, decapod shrimps, were mostly in their planktonic larval stage.

CONCLUSION.—*Apogon snyderi* is a nocturnal predator that feeds on both free-swimming and benthic forms, mostly crustaceans.

General Remarks on Cardinalfishes

Cardinalfishes are widely recognized as being nocturnal. For example, Starck and Davis (1966) reported that all of the apogonids they studied in Florida Keys are nocturnal, and Randall (1967) came to the same conclusion for species in the West Indies; Randall provided food-habit data on two forms, *Apogon conklini* and *A. maculatus,* both of which prey primarily on plankton.

In the Gulf of California, *A. retrosella,* a relatively small nocturnal species (mostly <100 mm long), aggregates above the reef at night, preys on plankton, and its aggregations are more compact under moonlight than on dark nights (Hobson, 1965, 1968a). Although the relatively large *A. menesemus* is solitary when feeding on free-swimming prey above Kona reefs, it remains within about 1 m of the reef, never far from cover.

Another apogonid occasionally seen in Kona, *A. maculiferus,* has behavior more like that of *A. retrosella* in the Gulf of California. *Apogon maculiferus* is abundant on some Hawaiian reefs and attains a length of about 150 mm (Gosline and Brock, 1960). It was not abundant during this study, however, and all those seen apparently were juveniles that ranged between about 20 and 60 mm long. On nights of bright moonlight these small individuals were in aggregations 2 to 3 m above the reef; however, on dark nights they ranged even higher in the water column, their aggregations were more loosely formed, and many of them were solitary. Significantly, limited observations indicate that juveniles of both *A. menesemus* and *A. snyderi* (<50 mm long) behave more like these small individuals of *A. maculiferus* than they do like the adults of their own species, so this behavior may be characteristic only of the smaller representatives of all three species.

Finally, a fourth apogonid, *Pseudamiops gracilicauda,* is relatively numerous in Kona, but does not seem to grow longer than about 30 mm. Being such a small species, *P. gracilicauda* generally went unnoticed by me and, in fact, was seen only on dark nights when solitary individuals hovered 1 to 2 m above the reef.

Suyehiro (1942), Hiatt and Strasburg (1960), and Hobson (1965), all reported that certain apogonids cease to feed sometime during reproductive activity. Perhaps this phenomenon accounts for the relatively high incidence of empty stomachs at night in *A. menesemus* from Kona (15 of 40), especially considering that species of other nocturnal groups with similar diets, like the various holocentrids (see above), are almost always full of food at night.

E. H. Chave, University of Hawaii, is currently working on the ecology of Hawaiian apogonids.

Family Carangidae: jacks

The jacks are prominent fishes on Hawaiian reefs, but although many species were seen occasionally during this study, only one, presented below, was observed regularly.

Caranx melampygus Cuvier—blue ulua, *'omilu*

This jack (Figure 21), attains a length of about 1 m in Hawaii (Gosline and Brock, 1960), but most of those present in Kona during this study were less than half this size. During the day it usually is solitary, or in groups of several individuals. Typically, it swims actively about 1 m above the reef in a manner that suggests it is patrolling over a relatively large area. Frequently several of these jacks accompany the large piscivorous goatfish, *Parupeneus chryserydros* (see account for this species, below), probably to capture prey that are driven out of hiding as the goatfish probes the substratum. This jack swims over the reef throughout the day, but occurs there most frequently during early morning and late afternoon

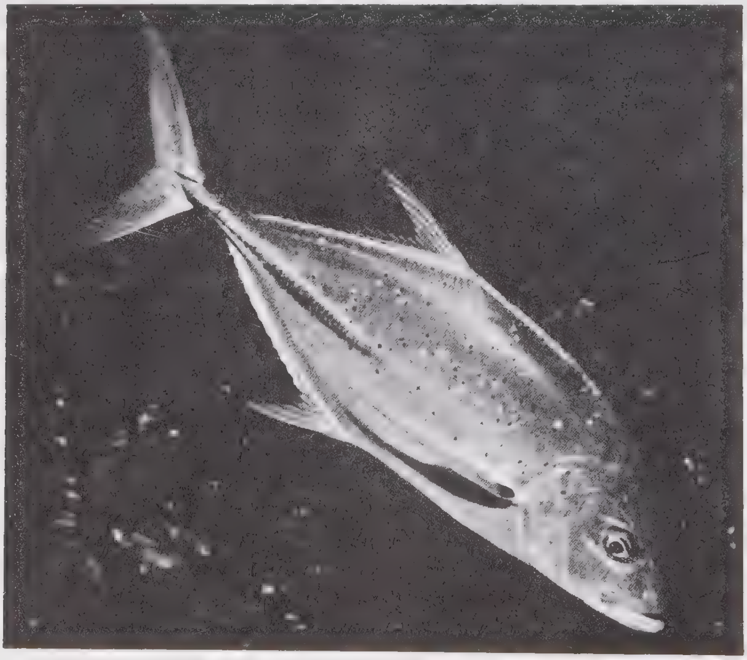


FIGURE 21.—*Caranx melampygus,* a jack, swimming close above the reef during the day.

or evening. It was only occasionally seen at night, perhaps because it avoided our diving lights after dark.

Six specimens (337: 245-570 mm) were collected at various times of the day. The only one (248 mm) that contained relatively fresh prey (three larval fishes, about 10 mm long, and a number of mysids) was collected 3 h after sunrise. A second individual (315 mm), taken shortly after noon, contained in its stomach, an unidentified fish (about 80 mm) and a shrimp, both moderately digested. Three other individuals (245-330 mm) were collected late in the afternoon, and their stomachs contained well-digested fragments—in at least one, the fragments of a fish. The last specimen (570 mm) behaved as if sick when speared early in the afternoon, and its gut was empty. Hiatt and Strasburg (1960) found only fishes in the two specimens of this species that they examined from the Marshall Islands, as did Randall (1955) in the four specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Caranx melampygus* preys on free-swimming fishes and crustaceans, probably most often early and late in the day.

General Remarks on Jacks

Jacks are major predators on many widespread tropical reefs (e.g. Marshall Islands: Hiatt and Strasburg, 1960; Gulf of California: Hobson, 1965, 1968a; Florida Keys: Starck and Davis, 1966; West Indies: Randall, 1967). The larger piscivorous jacks, like *Caranx hippos caninus,* are primarily crepuscular in the Gulf of California (Hobson, 1965, 1968a) and in the Florida Keys (Starck and Davis, 1966).

Family Lutjanidae: snappers

As is true of the sea basses, Hawaiian inshore reefs lack native species of snappers, a family whose members are prominent on shallowwater reefs elsewhere in the tropical Pacific (Gosline and Brock, 1960; Randall and Brock, 1960). Only one species of this family was seen regularly on the Kona study reefs during this project.

Aphareus furcatus (Lacépède)—*gurutsu*

During the day this solitary predator swims slowly, 1 to 2 m above the reef, with never more than a few individuals in any one place. It was not seen at night during this study, perhaps because it avoided our lights. Only once did I see one attack prey: 5 min before sunrise this individual suddenly broke from its patrolling attitude 2 m above the reef and dived among a cluster of small fishes, mostly pomacentrids, that were in the process of emerging from their nocturnal shelters (see Hobson, 1972). The success of the strike was undetermined, but at the instant of attack all small fishes within a radius of about 15 m shot under cover.

Three specimens (253: 244-262 mm) were speared for study. One taken during midafternoon contained a *Plagiotremus goslinei,* a blenny that swims above the reef only in daylight (see account for this species, below); because this prey was relatively fresh, it almost certainly was captured earlier that day. Another *A. furcatus* collected during midafternoon contained moderately digested crab megalops and gammaridean amphipods; although megalops are more typically food of nocturnal predators, the relatively good condition of these small prey indicated they had been collected earlier that day. The third *A. furcatus,* speared during midmorning, was empty. Randall (1955) examined four specimens of this snapper in the Gilbert Islands, and the two with prey contained only fishes.

CONCLUSION.—*Aphareus furcatus* preys on free-swimming fishes and crustaceans during daylight. Its habits at night remain unknown.

General Remarks on Snappers

If *Aphareus furcatus* hunts prey mostly in daylight, it would seem an atypical lutjanid. Generally lutjanids are described as nocturnal fishes (e.g. Hobson, 1965, 1968a: Gulf of California; Starck and Davis, 1966: Florida Keys; Randall, 1967: West Indies).

The efforts that successfully introduced the sea bass *Cephalopholis argus* into Hawaiian waters (see account for that species, above) also included the snapper *Lutjanus vaigiensis*, which now too is well established in Kona. Although *L. vaigiensis* was not numerous in the study area during this work, one school was seen consistently during daylight on irregular visits to a location in Kealakekua Bay, and solitary individuals occasionally were encountered on the reef after dark. Thus, the habits of this fish appear to be similar to those of certain other species of *Lutjanus* elsewhere; that is, it forms relatively inactive schools during the day, then disperses at nightfall and hunts prey after dark. This pattern is known for *L. argentiventris* in the Gulf of California (Hobson, 1965, 1968a), and for *L. griseus* and others in the tropical Atlantic (Starck and Davis, 1966). Randall and Brock (1960) reported predominantly nocturnal feeding by *L. vaigiensis* in Tahiti and often found this snapper in large aggregations during the day.

Family Sparidae: porgies

Monotaxis grandoculis (Forskål)—*mu*

In Kona, this porgy is most numerous near basalt reefs that are exposed to the prevailing sea. During the day it typically hovers 2 to 3 m above the reef, either in loose aggregations of 4 to 10 fish, or as solitary individuals. When congregated, most individuals display broad bars on their sides dorsally; although this same color pattern occurs frequently in solitary fish, these often are overall pale grey. Those I observed in Kona during the day always seemed inactive; however, Hiatt and Strasburg (1960) reported individuals in the Marshall Islands excavating prey buried in the sand, presumably during daylight. In Kona, *M. grandoculis* disperses from its daytime assemblages at nightfall and forages as solitary individuals throughout the night. After dark, many move into shallower water than is frequented by the species in daylight. The nocturnally active individuals sometimes show the barred color pattern but are most often plain grey (Figure 22).

Of five specimens (312: 244-397 mm) speared during day and night, one that was taken from an aggregation late in the afternoon was empty, whereas all four that were speared at night (later than 4 h after sunset and before first morning light) were full of food, as listed in Table 22.

Although the gut contents were relatively fresh, the shelled items had been reduced to crushed fragments—presumably by the large molarform jaw teeth of this fish.

Prey taken by this porgy in Kona are much the same as taken by the same species in the Marshall Islands (Hiatt and Strasburg, 1960) and Gilbert Islands (Randall, 1955).

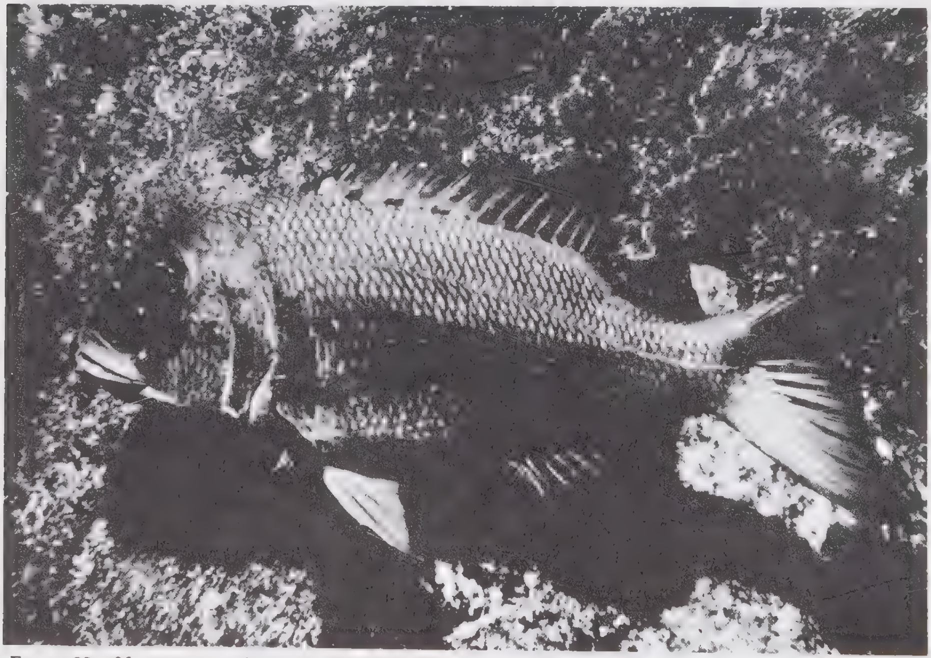


FIGURE 22.—*Monotaxis grandoculis*, a porgy, showing its plain grey coloration as it swims close to the reef at night.

TABLE 22.—Food of *Monotaxis grandoculis*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	4	21.3	21.30
2	Ophiuroids	3	27.1	20.33
3	Echinoids	3	21.3	15.98
4	Opisthobranch gastropods	2	11.8	5.90
5	Pagurid crabs	2	3.8	1.90
6	Polychaetes	1	3.8	0.95
7	Brachyuran crabs	1	2.5	0.63
8	Tunicates	1	2.5	0.63
9	Egg masses (unident.)	1	1.3	0.33
10	Holothurians	1	0.8	0.20
Also,	crustacean fragments	1	2.5	0.63
	Algal fragments	1	1.3	0.33

CONCLUSION.—*Monotaxis grandoculis* is a nocturnal predator that feeds on benthic invertebrates, most of them heavily shelled.

General Remarks on Porgies

Porgies are closely related to the snappers, most of which seem to be mainly nocturnal. Nevertheless, porgies have been reported as diurnal, for example species of *Archosargus*, *Diplodus*, and *Calamus* in the tropical Atlantic (Randall, 1967). Still, Starck and Davis (1966) recognized that species of *Calamus* in Florida may also feed at night. Diurnal habits in porgies may be attributed to their habit of excavating buried prey, which makes available to them certain nocturnal forms that have concealed themselves in the sand during daylight.

Family Mullidae: goatfishes

Mulloidichthys auriflamma (Forskål)—*weke'ula*

During the day this goatfish, which is relatively numerous in Kona, hovers in schools above the reef, or (occasionally) under ledges. Individuals recognized by distinguishing marks occurred in schools at the same locations each day, even though these schools disperse at nightfall. After dark, solitary or in small groups, this species probes with its barbels in the sandy areas adjacent to the reef, and in some of the larger sand patches on the reef. When illuminated by a diving light at night, it often shows a deep reddish hue that seems to be a reaction to the light, not a nocturnal coloration.

Of the 22 individuals (170: 110-235 mm) speared during day and night, all 12 collected from schools during the afternoon were either empty or contained only well-digested fragments, whereas of the 10 collected at night (later than 3 h after sunset and before sunrise), all contained food, including fresh material, as listed in Table 23.

Thus my observations concur with those of Gosline and Brock (1960), who reported that *M. auriflamma* does not feed during the day, but instead schools quietly in certain established areas and then disperses to forage at night.

Although crab megalops, a primary food, are a major element of the plankton, most of those captured by this goatfish probably were taken from the sand.

CONCLUSION.—*Mulloidichtys auriflamma* is a nocturnal predator that feeds on invertebrates that live in the sand.

Mulloidichthys samoensis (Günther)—*weke 'a'a*

This goatfish, widespread in Kona, often hovers in quiet schools over the reef during the day, where it looks much like *M. auriflamma*, above. Although *M. samoensis* is a more elongated fish, the two must be seen together before this distinction is obvious. Sometimes the two species school together, but more often they are segregated. Frequently instead of schooling during the day, *M. samoensis*, but not *M. auriflamma*, moves as solitary individuals or in small groups over sand patches on the reef, and there actively probes with its barbels in the sediment. These active individuals have a color pattern distinct from that of relatively inactive conspecifics in schools. When schooling, *M. samoensis* has a prominent yellow stripe running from eye to tail along its upper sides, as does *M. auriflamma* in similar schools (Figure 23a); however, this stripe is not present (or at least is indistinct) when *M. samoensis* actively

TABLE 23.—Food of *Mulloidichthys auriflamma*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Crab megalops	6	11.5	6.90
2	Ophiuroids	4	14.5	5.80
3	Polychaetes	4	11.7	4.68
4	Xanthid crabs	6	7.0	4.20
5	Prosobranch gastropods	7	4.7	3.29
6	Echinoids	6	4.7	2.82
7	Gammaridean amphipods	5	1.3	0.65
8	Isopods	4	1.1	0.44
9	Ostracods	2	0.6	0.12
10	Sipunculid introverts	1	0.5	0.05
11	Pelycypods	1	0.5	0.05
12	Penaeid shrimps	1	0.5	0.05
13	Portunid crabs	1	0.2	0.02
Also,	crustacean fragments	4	8.5	3.40
	Unidentified fragments	2	12.0	2.40
	Algal fragments	1	1.0	0.10
	Sand, foraminiferans, and debris	7	19.7	13.79

forages on the reef, it being replaced by a black spot on the fish's side, below the dorsal fin (Figure 23b).

At nightfall, those individuals of *M. samoensis* that had been hovering over the reef in quiet schools disperse. After dark the species not only continues the activity that some members had pursued over reef sand patches in daylight, but also extends this activity in some areas farther out over the more extensive sandy areas adjacent to the reef. When illuminated by a light at night, *M. samoensis* frequently displays a color pattern of red blotches that seems to be a response to the light, rather than being a nocturnal color feature. Its coloration at night is as described above for foraging individuals in daylight. After a night of foraging, many individuals regroup in the morning, forming schools that reappear in the same locations each day.

Twenty-three specimens (182: 136-283 mm) were speared during day and night. Of four taken during afternoons as they probed sand patches on the reef, swimming in small groups or as individuals, two had full stomachs that included relatively fresh prey; the other two contained only debris. Of three individuals taken while they hovered in schools over the reef during the afternoon, one had an empty stomach, and the other two contained only well-digested fragments. Contrasting data were provided by 16 specimens speared as they actively probed in sand patches on the reef during the 2 h immediately before first morning light, and during the first 30 min of morning twilight. Of these, 11 had full stomachs, including much fresh material, 2 contained only bits of debris, and only 3 were empty. Items in the 13 individuals containing identifiable prey are listed in Table 24.

No obvious difference was noted between prey taken during day and night although pertinent data are too few for meaningful comparison. Hiatt and Strasburg (1960) reported that fishes are an important food of this goatfish in the Marshall Islands. Otherwise, they listed foods similar to those taken by the species in Kona.

CONCLUSION.—*Mulloidichthys samoensis* preys on sand-dwelling invertebrates, mostly at night, but to some extent during the day.

Parupeneus multifasciatus (Quoy and Gaimard) —*moano*

This is the most numerous and widespread goatfish on Kona reefs. During the day solitary individuals and groups of two or three actively probe with their barbels among cracks and crevices on the reef, especially in pockets where sand and debris have accumulated. This species is active through twilight, but generally appears inactive after dark, when solitary individuals rest in exposed locations on the reef. To some extent these immobile nocturnal attitudes may be influenced by the diving light, but not to the extent indicated for *P. bifasciatus*, below; certainly the blotched red color pattern often displayed at this time is a reaction to the light. On nights of bright moonlight, at least some individuals of *P. multifasciatus* swim over the reef.

Thirty specimens (162: 125-212 mm) were speared during day and night. Of 14 collected during the hour immediately before first morning

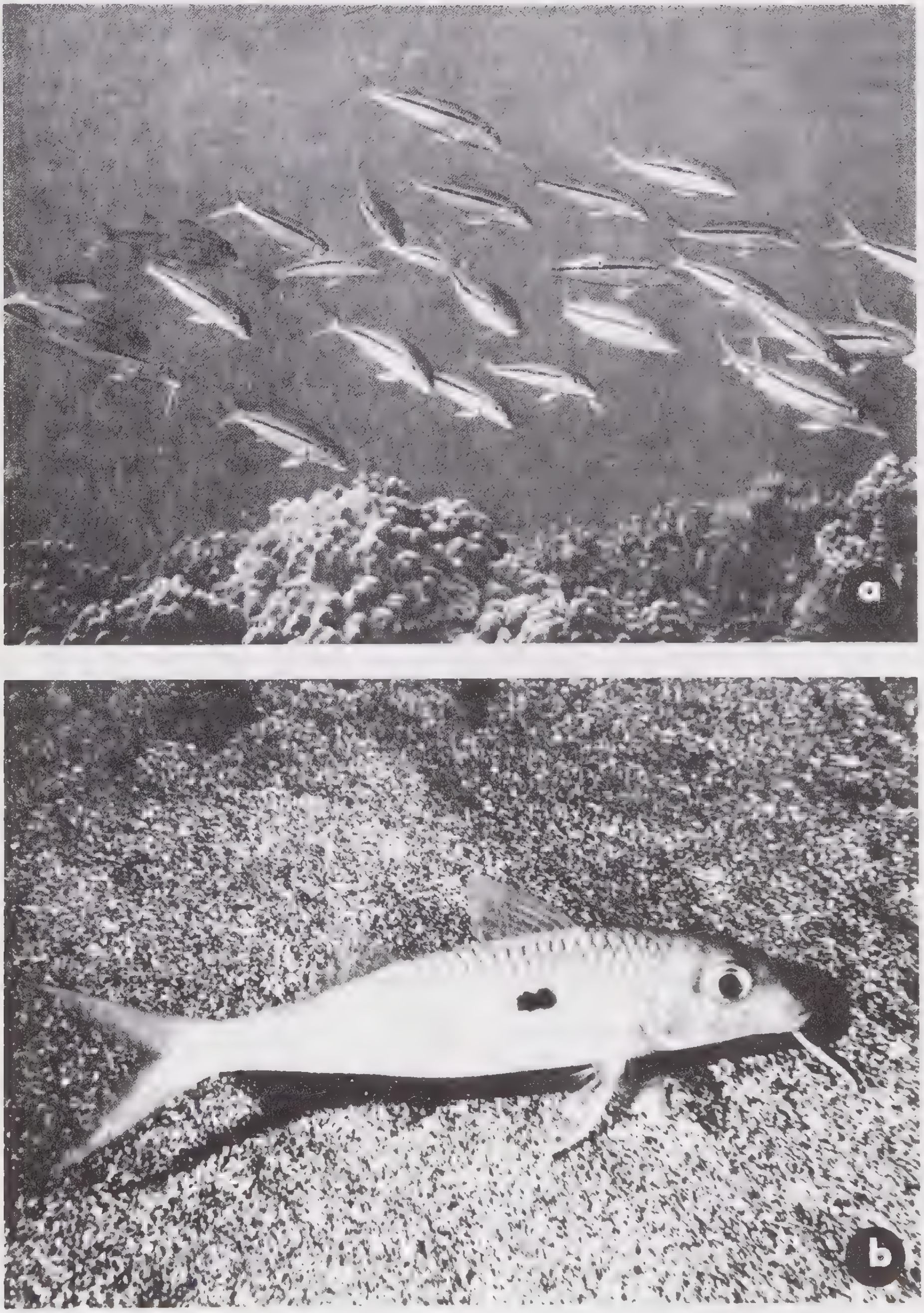


FIGURE 23.—*Mulloidichthys samoensis*, a goatfish: a, with the coloration shown when schooling during the day; b, with the coloration shown when feeding as a solitary individual or in small groups during both day and night.

TABLE 24.—Food of *Mulloidichthys samoensis.*

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Pelecypods	7	10.0	5.39
2	Polychaetes	5	11.2	4.31
3	Gammaridean amphipods	7	6.7	3.61
4	Prosobranch gastropods	6	3.1	1.43
5	Sipunculid introverts	3	5.4	1.25
6	Crab megalops	3	3.1	0.72
7	Isopods	3	2.8	0.65
8	Hippid crabs	1	0.8	0.06
9	Echinoids	1	0.8	0.06
10	Xanthid crabs	1	0.4	0.03
11	Shrimps	1	0.2	0.02
Also,	crustacean fragments	5	7.1	2.73
	Unidentified fragments	3	11.6	2.68
	Sand and debris, including foraminiferans	13	36.8	36.80

TABLE 25.—Food of *Parupeneus multifasciatus.*

Rank	Items	No. fish with this item (n = 18)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	14	30.6	23.80
2	Caridean shrimps	8	15.4	6.84
3	Crab megalops	5	8.6	2.39
4	Prosobranch gastropods	3	1.8	0.30
5	Tanaids	2	0.6	0.07
6	Gammaridean amphipods	2	0.4	0.04
7	Stenopid shrimps	1	0.6	0.03
8	Ostracod	1	0.1	0.01
Also,	crustacean fragments	14	29.4	22.87
	Unidentified fragments	1	0.8	0.04
	Debris	7	11.7	4.55

light, and through morning twilight, the stomachs of 12 were empty, but the other 2 contained prey in varying stages of digestion that appeared to have been taken during the night (one night with, the other without, moonlight). In contrast, all 16 specimens speared on the reef during the afternoon contained prey in varying stages of digestion, including fresh material. Items in the 18 containing identifiable material are listed in Table 25.

No obvious difference in diet was noted between the 2 individuals of *P. multifasciatus* that apparently had captured their prey at night and the 14 that had been feeding in daylight; however, the data are too few for a meaningful comparison.

Juveniles of *P. multifasciatus* sometimes aggregate up in the water column where plankton abounds, apparently feeding on these organisms, but none of these individuals were collected. The relatively high incidence of crab megalops in the diet of this and other bottom-feeding goatfishes may reflect some predation on free-swimming forms in the water column, but I believe that at least most of these megalops were taken off the sea floor.

CONCLUSION.—*Parupeneus multifasciatus* is primarily a diurnal predator that takes benthic crustaceans.

Parupeneus bifasciatus (Lacépède)—*munu*

This goatfish, which exceeds 300 mm when fully grown, is especially numerous among basalt boulders—frequently solitary, but also in groups of two or three. In daylight, its actions appear much like those of *P. multifasciatus,* which it resembles, but after dark, when *P. multifasciatus* generally rests on the reefs, *P. bifasciatus* usually moves about. Nevertheless, when *P. bifasciatus* is illuminated by the diving light it often settles immobile onto the reef—an action that complicates assessing its nocturnal activity. Like *P. multifasciatus, P. bifasciatus* often displays at this time a blotched red-colored pattern that seems to be a response to the diving light.

Twenty-seven specimens (229: 164-300 mm) were speared during day and night. Of 11 taken as they swam close to the reef during early morning (between first light and 3 h after sunrise), the stomachs of 2 were empty, but the other 9 contained prey in varying stages of digestion, some of it fresh. Similarly, of 12 individuals collected as they swam close to the reef during afternoons, only 1 had an empty stomach, whereas the other 11 contained prey in varying stages of digestion, some of it fresh. Finally, of four specimens speared at night (between 4 and 5 h after sunset) the stomach of one was empty, but the other three contained prey in varying stages of digestion, some of it fresh.

These data indicate that *P. bifasciatus* feeds regularly during both day and night. Recognizing that the contrasting conditions under which it hunts may be reflected in the composition of its diet, I attempted to distinguish prey that had been taken by day from that taken at night. Although, undoubtedly there is overlap, generally specimens collected during the night and early morning should contain mostly prey captured after dark, whereas specimens taken during afternoons should contain mostly prey taken in daylight.

Thus, the 12 *P. bifasciatus* taken during the night and early morning with identifiable material in their stomachs presumably represent mostly nocturnal feeding. Items in these individuals are listed in Table 26. Using the same rationale, diurnal feeding presumably is reflected in the 11 *P. bifasciatus* collected with identifiable material in their stomachs during afternoons. Items in these individuals are listed in Table 26.

Although xanthid crabs are the major prey day and night, they assume greater relative importance in daylight, as do caridean shrimps. Xanthids and carideans are largely under cover in daylight, where they may be especially vulnerable to this predator's probing actions. Crab megalops become increasingly important to this goatfish at night, but the circumstances surrounding their capture remain uncertain; megalops are the major prey of many nocturnal planktivores, such as *Myripristis* spp. (see accounts for these species, above), but are also taken day and night by predators like certain goatfishes that probe the sea floor.

Based on the above data, fishes seem to be more available as prey to *P. bifasciatus* at night. Prey fishes that could be identified were blennies and pomacentrids, which are diurnal fishes that take cover after dark. Apparently *P. bifasciatus* is adapted to capture these resting diurnal fishes at night, but is less effective in capturing the fishes that are under cover during daylight.

CONCLUSION.—*Parupeneus bifasciatus* hunts prey on the reef during both day and night. Adult crabs and shrimps are more important as prey during the day than at night, whereas the reverse is true of fishes and crab megalops.

Parupeneus porphyreus (Jenkins)—*kumu*

This is the most numerous goatfish on some Hawaiian reefs (Gosline and Brock, 1960), but

TABLE 26.—Food of *Parupeneus bifasciatus*.

Nighttime Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	10	29.0	24.17
2	Fish	6	17.0	8.50
3	Crab megalops	5	19.4	8.08
4	Caridean shrimps	7	8.0	4.67
5	Octopods	2	3.9	0.65
6	Oxyrhynchid crabs	2	1.7	0.28
7	Prosobranch gastropods	2	0.6	0.10
8	Polychaetes	1	0.4	0.03
9	Gammaridean amphipods	1	0.3	0.03
Also, crustacean fragments		7	15.5	9.04
	Debris	2	4.2	0.70
Daytime Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	9	43.3	35.43
2	Caridean shrimps	9	15.5	12.68
3	Crab megalops	3	3.5	0.95
4	Octopods	1	7.1	0.65
5	Grapsid crabs	1	3.9	0.35
6	Oxyrhynchid crabs	1	1.1	0.10
7	Fish	1	0.7	0.06
8	Gammaridean amphipods	2	0.2	0.04
Also, crustacean fragments		8	24.7	17.96

there are relatively few in the Kona study area. During the day this species stays close to cover, where it usually occurs in small groups under ledges. At night solitary individuals are active close among rocks and coral on the reef.

Of the 11 specimens (157: 137-173 mm) collected, 6 speared close to reef crevices late in the afternoon either were empty or contained only a few well-digested fragments, whereas all 5 collected in the same places within 1 h after sunrise had stomachs full of prey, some of it fresh, as listed in Table 27.

CONCLUSION.—*Parupeneus porphyreus* is a nocturnal predator that feeds mostly on benthic crustaceans.

Parupeneus chryserydros (Lacépède)—*moano kea*

The scientific name of this goatfish remains uncertain. I follow Gosline and Brock (1960) in recognizing the nominal *P. chryserydros*, even though some authors (e.g. Lachner, 1960) refer this form to *P. cyclostomus* (Lacépède). Growing to about 600 mm long (Gosline and Brock, 1960), *P. chryserydros* is the largest of the goatfishes occurring regularly on Kona reefs.

During the day, solitary individuals or groups of two to five move over the reef, where their exceptionally long barbels work through the covering on rocky substrata. More often than not, groups of *P. chryserydros* are accompanied by a single jack, *Caranx melampygus*, which follows close behind them. For 1 mo I recorded all sightings of *P. chryserydros* that swam in groups of two or more, and of 24 such groups, 16 were accompanied by a jack. Usually solitary individuals of this goatfish are not thus accompanied, but this too was seen four times during the month. Clearly, it is the jack that maintains the association, probably as a tactic to capture prey driven from cover as the foraging goatfish disturb the substratum. Apparently the jack finds this advantage only with *P. chryserydros*, as it was not seen similarly following other species. Titcomb and Pukui (1952) listed many ancient Hawaiian fish names which they were unable to associate with species recognized today. One of these, *moano ukali ulua,* translates as "moano with ulua following," and probably refers to *P. chryserydros*. Whereas the adults of *P. chryserydros* are followed by the jack, the juveniles of this goatfish frequently swim close beneath various labrids, especially *Thalassoma duperrey,* and here it is the goatfish that maintains the associations, though to what advantage I do not know.

Of the 20 specimens (261: 123-363 mm) collected, all 3 that were speared as they rested on the reef at night (between 4 h after sunset and first morning light) had empty guts, whereas 15 of 17 taken as they swam close to the reef at various times of the day (between midmorning and late afternoon) had prey in their stomachs, and only the other 2 were empty.

Fish were the major item, occurring in 13 of the 15 individuals that contained food (mean percent of diet volume: 83.1; ranking index: 72.02). Other food items were: xanthid crabs in two individuals (mean percent of diet volume: 8.3; ranking index: 1.11), caridean shrimps in one (mean percent of diet volume: 1.3; ranking index: 0.09), and unidentified fragments in two (mean percent of diet volume: 7.3; ranking index: 0.97).

The fishes in the diet ranged between 25 and 102 mm long, and included the following species: *Abudefduf imparipennis* (1), *Cirrhitops fasciatus* (2), *Istiblennius gibbifrons* (1), *Plagiotremus goslinei* (1), *Cirripectus* sp. (4), and a labrid (1). All of these are diurnal fishes that swim close to the reef in daylight, but take cover when a predator approaches. Judging by how *P. chryserydros* feeds,

TABLE 27.—Food of *Parupeneus porphyreus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	5	65.2	65.20
2	Hippid crabs	1	10.0	2.00
3	Caridean shrimps	1	2.0	0.40
4	Prosobranch gastropods	1	0.2	0.04
5	Chitons	1	0.2	0.04
6	Gammaridean amphipods	1	0.2	0.04
Also, crustacean fragments		3	21.2	12.72
	Debris	1	1.0	0.20

small fishes that have taken shelter on its approach probably are detected and even driven out from under cover by the exceptionally long barbels of this goatfish. If the probing barbels do in fact drive small fishes from their hiding places, this would account for the behavior of the jacks that follow them, described above. These same prey fishes also shelter themselves at night when they are inactive, so one might ask why this goatfish does not hunt for them at that time too. As reported above, *P. bifasciatus* preys on some of these same fishes (pomacentrids and blennies) when they are inactive under shelter at night. But capturing a relatively inert diurnal fish that is resting under cover after dark probably presents different problems for a predator than capturing an alert fish that has taken refuge from some specific threat in daylight. It appears that *P. bifasciatus* is adapted to taking these fishes when they rest under cover at night, whereas *P. chryserydros* is adapted to take them when they seek shelter in daylight. After dark, *P. chryserydros* is inactive, resting under reef cover (Figure 24).

Parupeneus cyclostomus in the Marshall Islands, which is closely related to *P. chryserydros*, if not conspecific, was reported by Hiatt and Strasburg (1960), on the basis of 16 specimens, to be an "active feeder on small benthonic fishes," but may prey more heavily on crustaceans than does the Hawaiian form.

CONCLUSION.—*Parupeneus chryserydros* is a diurnal predator that feeds mostly on small fishes.

General Remarks on Goatfishes

Despite their superficial similarity, the various goatfishes behave distinctively. Some, such as *Mulloidichthys auriflamma* and *Parupeneus porphyreus*, are primarily nocturnal; others, including *P. chryserydros* and *P. multifasciatus*, are mostly diurnal; and still others, like *P. bifasciatus* and *M. samoensis*, regularly hunt prey during both day and night. One might suppose that fishes which probe the sea floor for food would be indifferent to changes associated with day and night, but obviously this is not so. Whether a given species of goatfish is primarily diurnal or nocturnal probably relates to the differential day-night habits of its specific prey. That some goatfishes are

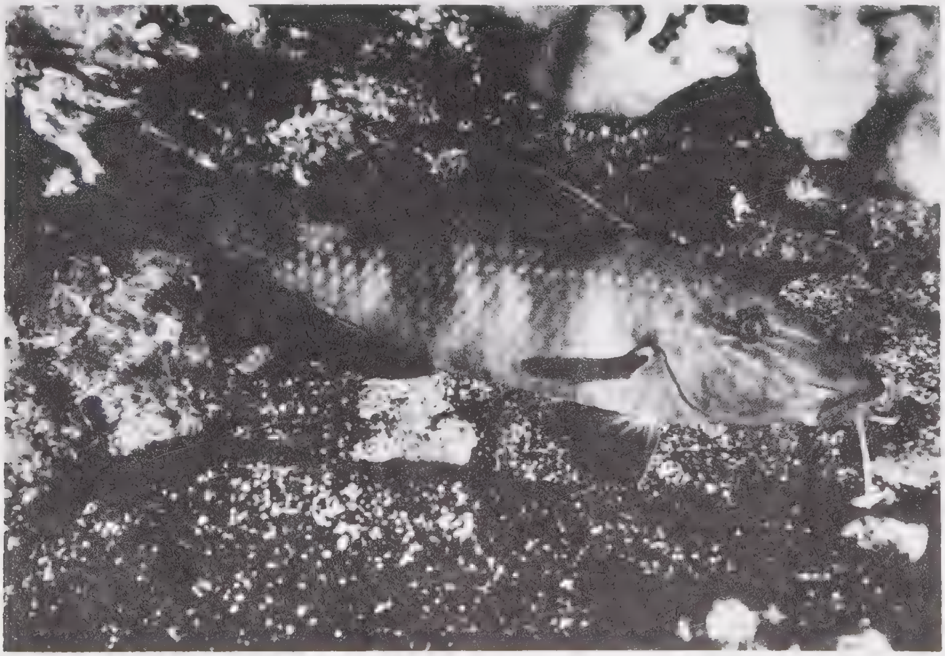


FIGURE 24.—*Parupeneus chryserydros*, a goatfish, resting under a ledge at night, with its exceptionally long chin barbels spread out before it.

nocturnal, whereas other are diurnal, is also recognized from other seas. In Florida, Starck and Davis (1966) suspected that *Mulloidichthys martinicus* feeds at night, whereas they recognized diurnal feeding habits in *Pseudupeneus maculatus*. Longley and Hildebrand (1941), as well as Collette and Talbot (1972), also regarded *M. martinicus* as nocturnal and *P. maculatus* as diurnal. Randall (1967) reported that *M. martinicus* feeds by day as well as night, and described a diet much like that of the two species of *Mulloidichthys* from Kona.

Family Kyphosidae: sea chubs

Kyphosus cinerascens Forskål—*nenue*

In Kona, *K. cinerascens* is most numerous where a basalt reef face confronts the prevailing swell in water deeper than about 8 m. Often over 500 mm long, this fish is active throughout the day—usually in groups of up to 10 or more individuals, and often swimming high in the water column. At night, solitary individuals swimming above the sea floor are often encountered in the same areas.

All three specimens (205: 166-250 mm) collected for study had guts full of a wide variety of benthic algae exclusively. Although two of these fish were taken during midday, the other was taken at night, within 1 h before first morning light. No sedimentary material was mixed in these gut contents, indicating that the algae had been bitten, not scraped, off the rocks, or else had been taken as fragments drifting in mid-water. Hiatt and Strasburg (1960) found the same gut contents in specimens from the Marshall Islands.

CONCLUSION.—*Kyphosus cinerascens* feeds during the day, cropping algae from rocks or taking them as drifting algal fragments. Its nocturnal habits remain uncertain.

General Remarks on Sea Chubs

Sea chubs generally are described as diurnal herbivores (e.g. Longley and Hildebrand, 1941; Starck and Davis, 1966; Randall, 1967). Smith (1907) reported crabs and bivalved mollusks among algae in the diet of *Kyphosus sectatrix* in the Atlantic Ocean, but these items probably were taken incidentally with the algae. Randall (1967) found only algae and a bit of sea grass in *K. sectatrix* from the West Indies. Starck and Davis (1966) reported that *K. incisor* rests in sheltered locations on Floridian reefs at night after having fed on drifting sargassum at the water's surface during the day. In the East Indies, however, William N. McFarland, Cornell University (pers. commun.) observed kyphosids active at night.

Family Chaetodontidae: angelfishes and butterflyfishes

The chaetodontids comprise two distinct groups: the angelfishes, subfamily Pomacanthinae; and the butterflyfishes, subfamily Chaetodontinae. Of the species treated below, the first two are angelfishes, the remainder are butterflyfishes.

Holacanthus arcuatus Gray—angelfish

This angelfish is sparsely distributed on Kona reefs, but being relatively large and distinctive is readily noticed where it occurs. Usually solitary or paired, it swims close among rock ledges and boulders at depths below about 8 m. During the day it picks material from the surface of rocks, but was not seen active at night.

Six specimens (136: 123-150 mm) were speared during afternoons, and all had full stomachs. They had fed almost exclusively on sponges (mean percent of diet volume and ranking index: 98.3). The only other items—algae and hydroids—probably were taken incidentally with the sponges.

CONCLUSION.—*Holacanthus arcuatus* is a diurnal species that feeds on sponges.

Centropyge potteri (Jordan and Metz)—potter's angelfish

An abundant species in coral-rich surroundings, this small angelfish behaves more like some of the damselfishes than it does other members of its family. A given individual limits its movements to restricted, well-defined locations close among fingerlike growths of the coral *Porites compressus*. During the day it swims about, picking at material growing over dead coral. At night it is alert, but secreted deep among the coral, apparently inactive.

All five specimens (80: 69-86 mm long) speared at various times during the day were full of food. Filamentous algae were the major identifiable item in the gut contents of all five (mean percent of diet volume and ranking index: 41.7). There also was much unidentified debris, including sand and foraminiferans (mean percent of diet volume and ranking index: 42.3) that all five apparently had scraped from the substratum, and which probably included substantial nourishment in the form of organic detritus. The other components of the diet, all minor, were: diatoms in all five (mean percent of diet volume and ranking index: 3.3), sponges in all five (mean percent of diet volume and ranking index: 2.3), and harpacticoid copepods in one (mean percent of diet volume: 0.3; ranking index: 0.06).

CONCLUSION.—*Centropyge potteri* is a diurnal species that feeds on benthic algae and probably on organic detritus.

Forcipiger flavissimus Jordan and McGregor—*lau wiliwili nukunuku 'oi 'oi*

This long-snouted species (Figure 25a), numerous in Kona, and widespread throughout the Indo-Pacific region, was long called *F. longirostris*. Only recently has the distinction between *F. flavissimus* and the true *F. longirostris* (Figure 25b and c; treated below) been recognized (Wheeler, 1964; Randall and Caldwell, 1970). *Forcipiger flavissimus* occurs singly, or, more often, in groups of two or three. It is active throughout the day, especially over coral-rich reefs, where it picks at objects on a variety of surfaces. At night it is alert close among rock and coral cover but apparently inactive.

Twenty-seven specimens (116: 94-137 mm) were speared during day and night. Of 11 that were taken either at night (later than 4 h after sunset) or during early morning twilight, the stomachs of 9 were empty, and those of 2 (collected between 4 and 5 h after sunset) contained only a few well-digested fragments. In contrast, all 16 specimens taken at various times of the day had full stomachs, including relatively fresh material, as listed in Table 28.

Most of the unidentified fragments among the gut contents were relatively fresh pieces that this fish apparently had recently torn from the bodies of larger animals. The similarity of its elongated snout and mouth to a pair of needle-nosed pliers (Figure 26, lower) underscores the adaptiveness of its feeding apparatus to this habit. Even the gripping surfaces on the pliers are paralleled in the snout of *F. flavissimus* by expanded contact-surfaces in both upper and lower jaws—both of which carry multiple rows of short, inwardly curving teeth (Figure 27b).

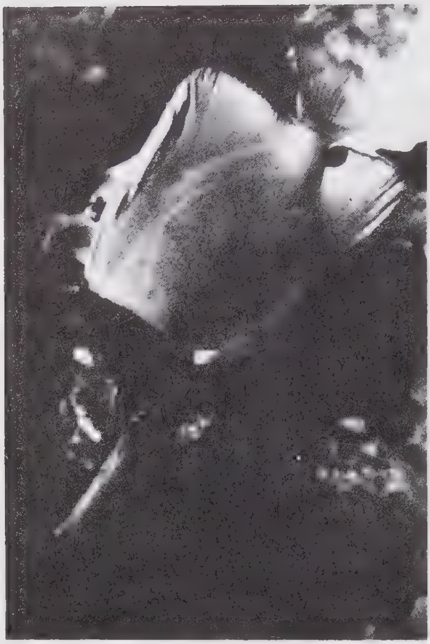
CONCLUSION.—*Forcipiger flavissimus* is a diurnal predator that tears pieces off larger benthic animals.

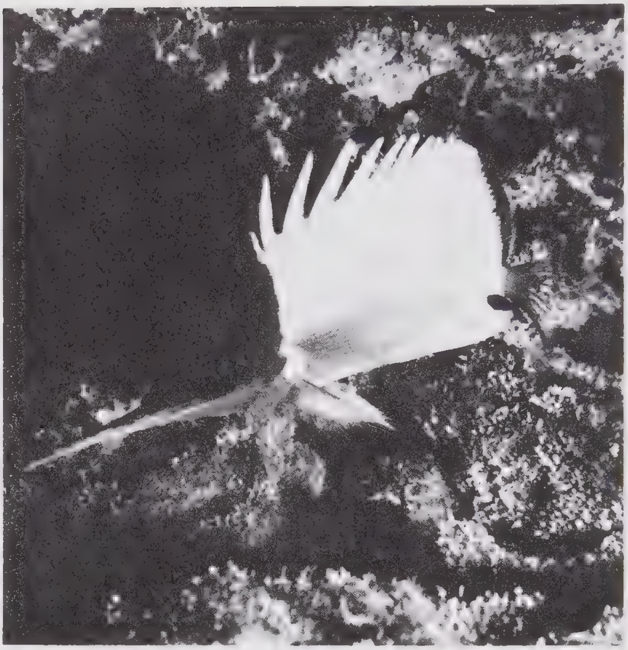
Forcipiger longirostris (Broussonet)—*lau wiliwili nukunuku 'oi 'oi*

This species is relatively numerous in Kona, although it appears to be rare elsewhere in Hawaii. Both color varieties—the yellow form (Figure 25b), which is essentially identical to *F. flavissimus,* discussed above, and the dark brown form (Figure 25c)—were observed regularly throughout the study. Like *F. flavissimus, F. longirostris* occurs typically over coral-rich reefs, and the two species overlap extensively; however, in areas where one is numerous, the other occurs less frequently. Despite this, I was unable to relate observed differences in relative numbers to specific habitat differences. *Forcipiger longirostris* is generally larger, but the most obvious morphological distinction between the two lies in the relative lengths of their snouts and in their different mouth structures (Figure 26). Less noticeable, but probably also related to feeding, *F. longirostris* has relatively larger eyes. Like its congener, *F. longirostris* is active on the reef by day, swimming singly or in groups of two or three, and probing with its long snout in cracks and crevices. At night it is close among cover of rocks or coral —alert, but apparently inactive.

Of the 26 specimens (136: 98-162 mm) collected, all 4 that were speared at night (later than 4 h after sunset and before first light in the morning) had empty stomachs, whereas the stomachs of all 22 collected at various times during the afternoon were full (including relatively fresh items). Decapod shrimps were the major prey, occurring in all 22 individuals that contained food (mean percent of diet volume and ranking index: 88.4). Other food items were: pagurid crabs, without the mollusk shell, in two individuals (mean percent of diet volume: 1.9; ranking index: 0.17), fish fragments in one (mean percent of diet volume: 0.5; ranking index: 0.02), and crustacean fragments in nine (mean percent of diet volume: 9.2; ranking index: 3.76).

In contrast to the omnivorous *F. flavissimus, F. longirostris* has a restricted diet. It does not tear





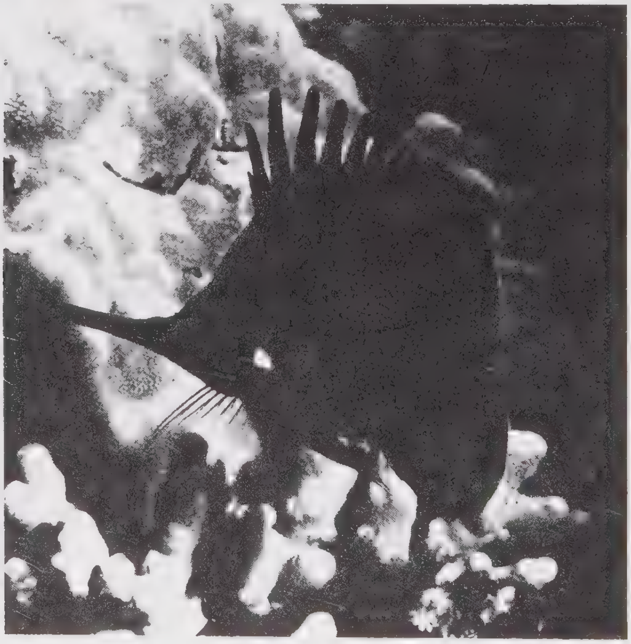


FIGURE 25.—a, *Forcipiger flavissimus*, a longsnouted butterflyfish, active on the reef during the day; b, *F. longirostris* (yellow form), a longsnouted butterflyfish, active on the reef during the day; c, *F. longirostris* (brown form), active on the reef during the day.

TABLE 28.—Food of *Forcipiger flavissimus*.

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Radioles of sabellid polychaetes	10	15.4	9.63
2	Nemerteans	7	11.9	5.21
3	Podia and pedicellaria of echinoids	9	7.0	3.94
4	Calanoid copepods	8	4.1	2.05
5	Tentacles of terebellid polychaetes	7	3.6	1.58
6	Gammaridean amphipods	7	2.3	1.01
7	Hydroids	8	1.0	0.50
8	Caridean shrimps	2	1.3	0.16
9	Caprellid amphipods	4	0.5	0.13
10	Sipunculid introverts	3	0.6	0.11
11	Prosobranch gastropod egg capsules	3	0.5	0.09
12	Crab megalops	2	0.1	0.01
13	Isopods	1	0.1	<0.01
14	Demersal fish eggs	1	0.1	<0.01
Also,	crustacean fragments	2	0.9	0.11
	Algal fragments	2	0.2	0.03
	Unidentified fragments	15	50.4	47.25

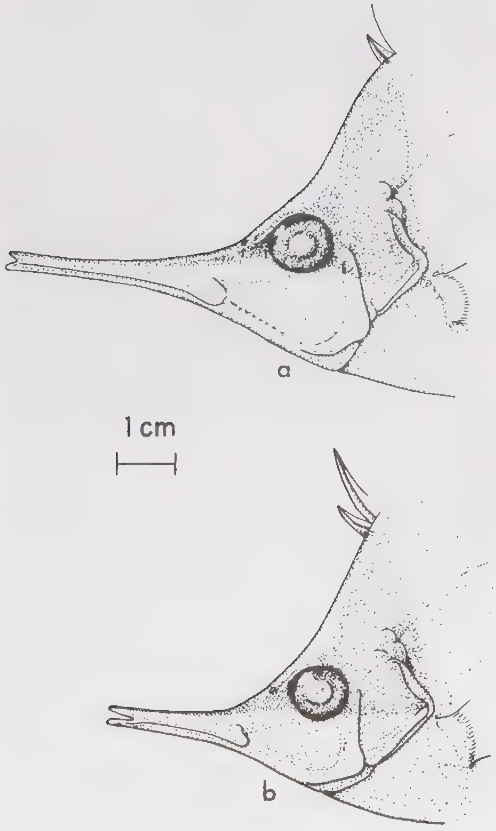


FIGURE 26.—The head and snout of: a, *Forcipiger longirostris*, 102mm long; *F. flavissimus*, 103 mm long. (Note: to discount the size difference in their snouts, lengths were measured from the posterior edge of the maxillary.)

off pieces of larger organisms, as does its congener, but instead takes only whole prey. The sharp difference between their diets is reflected in differing feeding structures. The snout and mouth of *F. longirostris* do not suggest needle-nosed pliers, as do those of *F. flavissimus;* indeed, for *F. longirostris,* the generic name *Forcipiger* (from the Latin *forcipis,* meaning pincers) is a misnomer. Compared with *F. flavissimus,* the mouth of *F. longirostris* is smaller and its jaws do not have the greatly expanded contact surfaces; the teeth are inwardly curved, as in *F. flavissimus,* but are longer and confined to only two or three rows at the front of the mouth (Figure 27a). Clearly, *F. longirostris* is adapted to grasping the tiny prey on which it feeds, but not to tearing pieces free.

CONCLUSION.—*Forcipiger longirostris* is a diurnal predator that takes small benthic animals, mostly decapod shrimps.

Hemitaurichthys thompsoni Fowler

This plain dark-brown chaetodontid seems to be generally rare in Hawaii (Gosline and Brock, 1960), but is numerous in several locations near

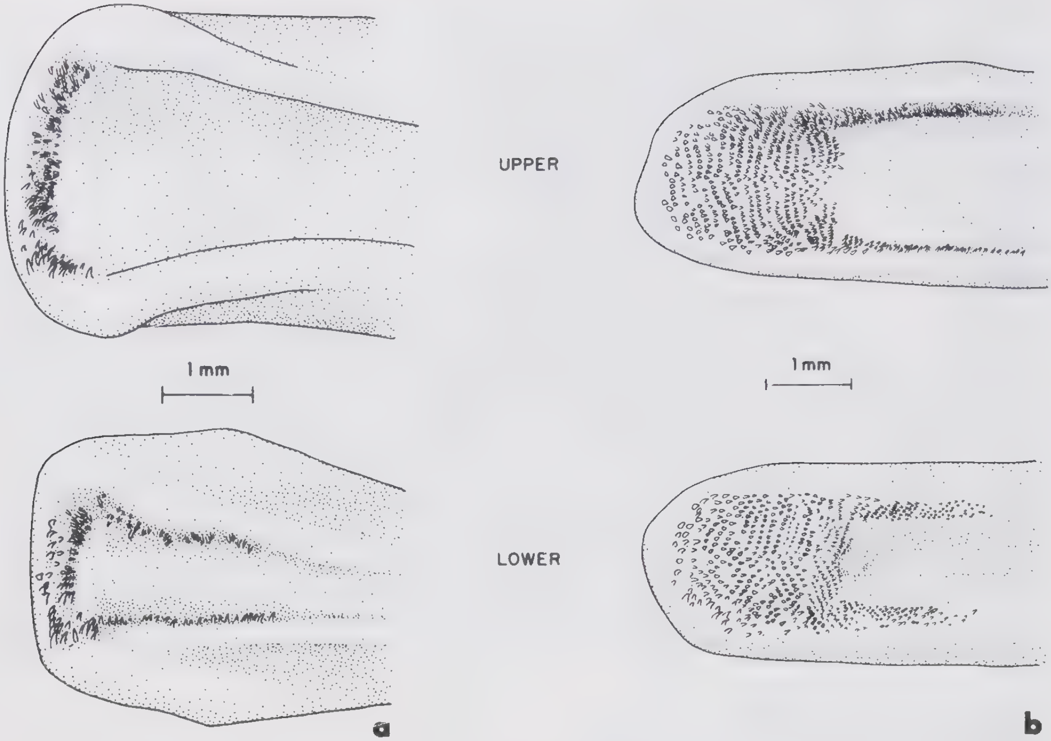


FIGURE 27.—Dentition of: a, *Forcipiger longirostris*; b, *F. flavissimus.*

the outer drop-off at Puuhonua Point, Honaunau. During the day it is active in large aggregations high in the water column, but at nightfall descends to the reef and remains close among cover until morning.

Of the 11 specimens (167: 127-185 mm) collected, all 5 that were taken from under cover on the reef at night (between 4 h after sunset and daybreak) had empty guts, whereas all 6 taken during afternoons from aggregations in midwater were full of food, as listed in Table 29.

I saw no evidence of benthic feeding by this fish. The circumstance that various planktonic copepods made up over 86% of its diet indicates that *H. thompsoni* is a more specialized feeder than its congener *H. zoster* below.

TABLE 29.—Food of *Hemitaurichthys thompsoni.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	6	81.9	81.90
2	Blue-green algae in gelatinous sacs	4	3.5	2.33
3	Cyclopoid copepods	4	3.5	2.33
4	Fish eggs, planktonic	4	1.0	0.67
5	Harpacticoid copepods	4	0.7	0.47
6	Hyperiid amphipods	3	0.3	0.15
7	Gastropods, planktonic	1	0.3	0.05
8	Unidentified egg masses in gelatinous matrix	1	0.2	0.03
9	Mysids	1	0.2	0.03
10	Larvaceans	1	0.2	0.03
Also, unidentified fragments		4	8.2	5.47

CONCLUSION.—*Hemitaurichthys thompsoni* is a diurnal planktivore that takes mostly copepods.

Hemitaurichthys zoster (Bennett)—blackface butterflyfish

Gosline and Brock (1960) stated that the colorful *H. zoster* (Figure 28a) and *H. thompsoni* attain a similar size (about 175 mm), but of those seen during this project, *H. zoster* was consistently smaller. Of the two, *H. zoster* also was by far the more numerous and more widespread. During the day *H. zoster* aggregates much like *H. thompsoni,* especially where the reefs drop abruptly into water deeper than about 10 m. Where *H. thompsoni* occurred, *H. zoster* was always nearby, but mixed aggregations of the two species were never seen. Unlike *H. thompsoni,* which was seen feeding only in mid-water, *H. zoster* sometimes is active in small groups close to the reef. At night *H. zoster* is generally solitary, close among cover in the same areas where it is active in daylight. Although *H. thompsoni* has the same coloration day and night, *H. zoster* displays a color pattern at night that differs strikingly from its daytime coloration (Figure 28a and b).

Twelve specimens (119: 100-128 mm) were collected during day and night. Four were speared during morning twilight from a group milling about close above the reef just prior to rising into mid-water. Two of these, taken 18 and 20 min before sunrise, respectively, both had empty stomachs; the third, taken 15 min before sunrise, contained calanoid copepods in varied stages of digestion; the fourth, taken 10 min before sunrise, contained more than 100 calanoid copepods and assorted other prey in varied stages of digestion. I cannot believe that all these prey had been taken since first light that morning, especially as no feeding was observed, and these fish had not yet risen to their customary plankton-feeding levels. And yet *H. zoster* was never seen above the reef at night. Until additional data are available, these two specimens remain anomalous. The other eight specimens, taken at various times during daylight from small aggregations above the reef, all had full stomachs. Items in the 10 individuals containing identifiable prey are listed in Table 30.

These data indicate that *H. zoster* has feeding habits that are less specialized than those of *H. thompsoni.* Planktonic copepods, constituting almost 62% of its diet, are still the major prey, but are less dominant than in *H. thompsoni.* Furthermore, *H. zoster* appears to feed significantly on benthic prey: the alcyonarian *Sarcothelia edmondsoni* constituted over 60% of the material in each of the three specimens in which it occurred.

CONCLUSION.—*Hemitaurichthys zoster* is chiefly a diurnal planktivore that takes primarily copepods, but also feeds on benthic organisms, especially alcyonarians.

Chaetodon corallicola Snyder

Observations in the western Pacific have indicated that the Hawaiian *C. corallicola* is closely related to, if not conspecific with, the widespread Indo-Pacific *C. kleini.* In Kona, this species is relatively numerous at depths below 20 m along the edge of the outer drop-off. In daylight it generally swims in loosely associated pairs that pick free-swimming organisms from the water column within a meter or so of the reef. At night it remains close among the coral—alert, but apparently inactive.

All 11 specimens (89: 75-96 mm) collected for study during afternoons had full stomachs (including fresh material), as listed in Table 31. The only evidence of bottom feeding among this material is the caprellid amphipods and hydroids, both taken from the same individual.

CONCLUSION.—*Chaetodon corallicola* is primarily a diurnal planktivore that feeds largely on copepods.

Chaetodon miliaris Quoy and Gaimard

Gosline and Brock (1960) noted that *C. miliaris* is one of the commonest inshore fishes. Although it is numerous in shallow water around Oahu, Brock and Chamberlain (1968), using a submarine off that island, found it even more abundant in deeper water. They discovered it to be a dominant form at depths below 120 m, where it hovered in aggregations 15 to 40 m above the sea floor, apparently feeding on plankton. In the Kona study area, this species rarely occurs in water shallower than 20 m, but is numerous along the outer drop-off at 30 m and deeper. During the day it aggregates 2 to 3 m above the reef, where it picks organisms from the plankton. At night it is scattered among the rocks and ledges, alert but apparently inactive.

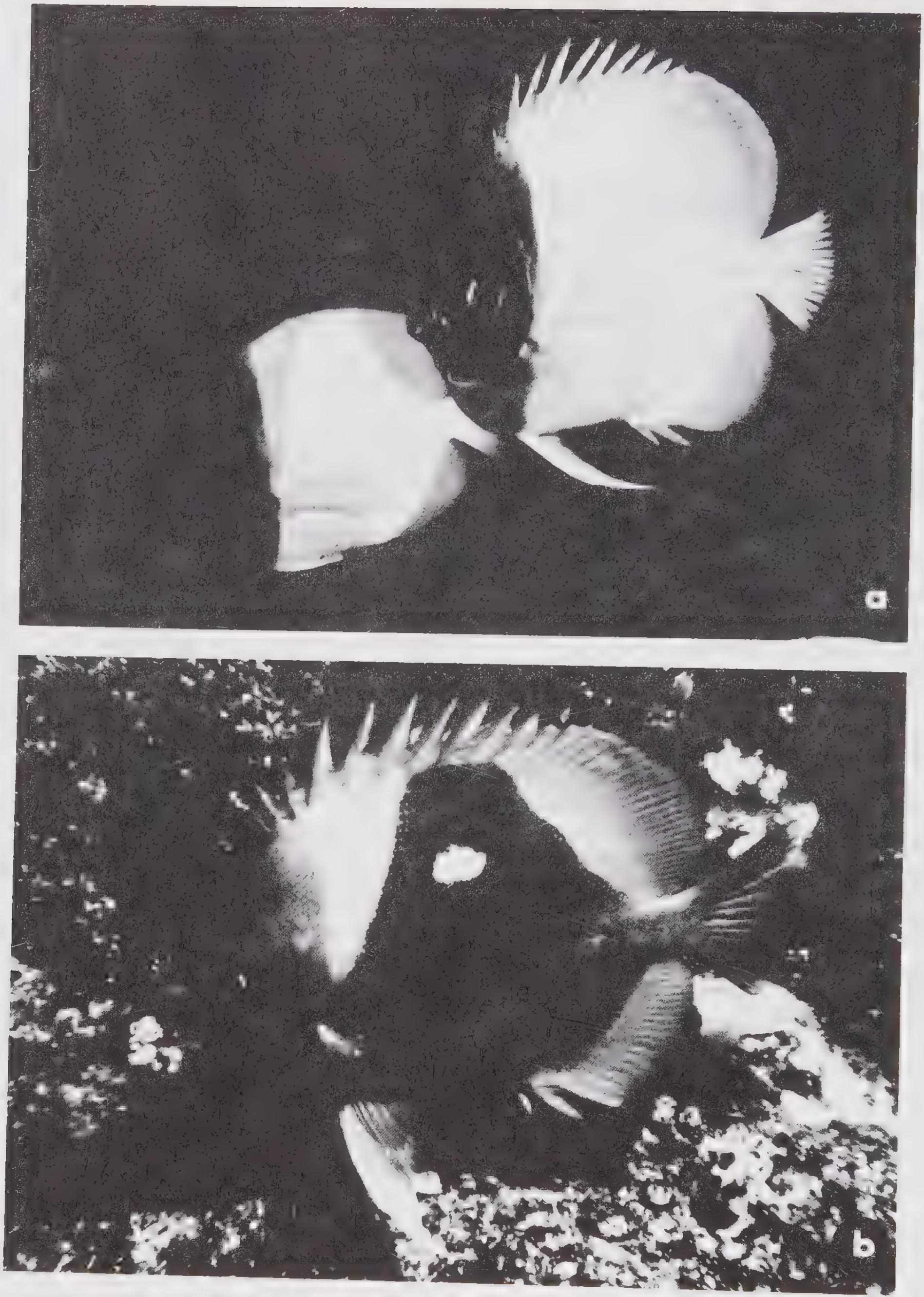


FIGURE 28.—*Hemitaurichthys zoster*, a butterflyfish: a, showing its diurnal coloration while swimming in the water column during the day; b, showing its nocturnal coloration while close to the reef at night.

TABLE 30.—Food of *Hemitaurichthys zoster*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	55.3	55.30
2	Alcyonarians	3	18.2	5.46
3	Cyclopoid copepods	8	6.1	4.88
4	Fish eggs, planktonic	6	1.9	1.14
5	Larvaceans	4	1.0	0.40
6	Blue-green algae in gelatinous sacs	3	1.3	0.39
7	Hydroids	2	1.9	0.38
8	Harpacticoid copepods	3	0.3	0.09
9	Gastropod veligers	2	0.3	0.06
10	Penaeid shrimps	1	0.2	0.02
11	Gastropod larvae, echinospira	1	0.1	0.01
12	Pelycypod larvae	1	0.1	0.01
13	Foraminiferans	1	<0.1	<0.01
14	Ostracods	1	<0.1	<0.01
Also, unidentified fragments		5	9.9	4.95
	Crustacean fragments	2	3.2	0.64

TABLE 31.—Food of *Chaetodon corallicola*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	52.6	52.60
2	Cyclopoid copepods	11	12.1	12.10
3	Fish eggs, planktonic	9	1.3	1.06
4	Larvaceans	2	5.5	1.00
5	Ostracods	3	0.5	0.14
6	Lobster phyllosomes	3	0.5	0.14
7	Mysids	2	0.3	0.06
8	Caprellid amphipods	1	0.5	0.05
9	Salps	1	0.2	0.02
10	Shrimp larvae	1	0.2	0.02
11	Hydroids	1	0.1	<0.01
12	Gammaridean amphipods	1	<0.1	<0.01
13	Blue-green algae in gelatinous sacs	1	<0.1	<0.01
Also, unidentified fragments		11	26.0	26.00

Of eight specimens (118: 110-125 mm) collected, one that was taken during early morning twilight close among cover contained only a few well-digested fragments, whereas all seven that were active above the reef when taken during the afternoon were full of food (much of it fresh), as listed in Table 32.

CONCLUSION.—*Chaetodon miliaris* is a diurnal planktivore that takes mostly copepods.

Chaetodon quadrimaculatus Gray—four-spot butterflyfish

This butterflyfish is especially numerous where the water is less than 10 m deep over reefs rich in the coral *Pocillopora*. During the day it is active, solitary or paired, close to the sea floor. Feeding strictly on the bottom, it mostly picks at the surface of living coral or in cracks within dead coral and basalt. It occurs in the same areas at night, but though alert, seems relatively inactive.

Twenty-six specimens (92: 43-110 mm) were speared during day and night. All 15 collected during midday were full of food, as were 4 of 5 taken at night during the 2 h immediately before midnight (the fifth was empty). The remaining six were collected at night during the hour immediately before daybreak, and while three of these had empty stomachs, the other three were full. Whether these findings indicate nocturnal feeding or slow digestion remains uncertain. No differences were recognized in composition or condition of gut contents between specimens taken day and night. Items in the 22 individuals containing identifiable material are listed in Table 33.

At least some of the corals taken by this fish probably are soft corals. Most material in the gut appeared as amorphous clumps rich in nematocysts and zooxanthellae. That much of this is soft coral seems likely considering how often *C. quadrimaculatus* nibbles about reef crevices where living stony corals are absent.

TABLE 32.—Food of *Chaetodon miliaris.*

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	7	68.6	68.60
2	Cyclopoid copepods	7	2.8	2.80
3	Salps	1	3.0	0.43
4	Hyperiid amphipods	3	0.4	0.17
5	Fish eggs, planktonic	3	0.4	0.17
6	Larvaceans	1	0.9	0.13
7	Egg masses in gelatinous sacs	2	0.4	0.11
8	Ostracods	1	0.1	0.01
9	Harpacticoid copepods	1	0.1	0.01
10	Mysids	1	0.1	0.01
Also, unidentified fragments		6	23.2	19.89

TABLE 33.—Food of *Chaetodon quadrimaculatus.*

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Anthozoans (no skeletal material)	22	81.4	81.40
2	Polychaetes (mostly tentacles and fragments)	13	6.2	3.66
3	Hydroids	13	1.6	0.95
4	Sipunculid introverts	7	1.9	0.60
5	Opisthobranch gastropods	3	1.3	0.18
6	Caprellid amphipods	6	0.4	0.11
7	Gammaridean amphipods	4	0.2	0.04
8	Cyclopoid copepods	2	0.1	<0.01
9	Calanoid copepods	1	<0.1	<0.01
10	Mites	1	<0.1	<0.01
11	Demersal eggs	1	<0.1	<0.01
Also, unidentified fragments		5	4.5	1.02
	Algal fragments, including diatoms	12	2.1	1.15

Opisthobranch gastropods had been taken by three of the individuals collected at night. Perhaps significantly, these same opisthobranchs are a major prey of *C. lunula* after dark (see below).

CONCLUSION.—*Chaetodon quadrimaculatus* feeds during the day mostly on corals, but also on polychaetes and other benthic organisms. Some nocturnal feeding is likely.

Chaetodon unimaculatus Bloch— one-spot butterflyfish

This chaetodontid is numerous on shallow reefs exposed to a strong surge where the coral *Pocillopora* is also abundant. Generally occurring in pairs, it is active during the day, picking at the surface of living *Pocillopora,* and to a lesser extent other reef surfaces. At night it is alert, but appears inactive as it hovers close among cover on the reef.

Twenty-six specimens (85: 66-102 mm) were speared during night and day. Of three that were collected during the 2 h immediately before midnight, two had empty stomachs, and the third contained a few well-digested fragments. Of four collected during the hour immediately before daybreak, two had empty stomachs, and two contained only well-digested fragments. Thus, there was no evidence of recent feeding by individuals taken after dark. In contrast, all 19 specimens collected during the day had full stomachs, including fresh material, as listed in Table 34.

The major food item, scleractinian corals (mostly *Pocillopora*), included many skeletal fragments.

CONCLUSION.—*Chaetodon unimaculatus* feeds during the day, mostly on the coral *Pocillopora.*

Chaetodon multicinctus Garrett— pebbled butterflyfish

Chaetodon multicinctus is probably the most numerous chaetodontid on Kona reefs in water

TABLE 34.—Food of *Chaetodon unimaculatus*.

Rank	Items	No. fish with this item (n = 19)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	15	45.3	35.76
2	Sponges	5	12.4	3.26
3	Gammaridean amphipods	4	1.3	0.27
4	Pelycypods	1	3.2	0.17
5	Sipunculid introverts	1	1.6	0.08
6	Calanoid copepods	2	0.3	0.03
	Also, unidentified fragments	18	29.1	27.57
	Algal fragments and diatoms	9	6.8	3.22

TABLE 35.—Food of *Chaetodon multicinctus*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Scleractinian coral polyps	11	91.6	91.60
2	Gammaridean amphipods	7	1.8	1.15
3	Sipunculid introverts	5	1.3	0.59
4	Polychaetes (fragments and tentacles)	3	0.4	0.11
5	Hydroids	2	0.2	0.04
6	Calanoid copepods	1	0.1	0.01
	Also, unidentified fragments	2	3.4	0.62
	Algal fragments and diatoms	6	1.2	0.66

shallower than 20 m, especially where stony corals abound. During the day it generally occurs in pairs, and is active close to the reef, often picking at living corals—both *Porites* and *Pocillopora*. At night it rests close among cover on the reef, alert but apparently inactive.

Of the 26 specimens (84: 78-94 mm) examined, all 15 that were collected at night (between 4 h after sunset and first morning light) were empty, whereas all 11 that were collected during midday were full of food (including fresh material), as listed in Table 35.

More so than the other butterflyfishes that feed on stony corals, *C. multicinctus* does so without also taking fragments of the surrounding skeleton.

CONCLUSION.—*Chaetodon multicinctus* is a diurnal predator that feeds primarily on scleractinian corals (mostly *Porites* and *Pocillopora*).

Chaetodon ornatissimus Solander—ornated butterflyfish

This butterflyfish is numerous over coral-rich reefs, generally swimming in pairs during the day. It moves from one growth of coral to another, locating and working its mouth over abrasions on the surface of the coral. In this way it feeds on a variety of scleractinian corals, including *Porites, Pavona,* and *Cyphastrea*. At night it rests quiet, but alert, close among cover on the reef. Its daytime and nighttime colorations differ strikingly (Figure 29a and b).

Nineteen specimens (119: 95-140 mm) were examined. All eight that were collected at night, later than 4 h after sunset and before first morning light, had the stomachs and anterior half of the intestines empty. All four that were taken during morning twilight—the earliest 25 min before sunrise—had material in their stomachs, but their intestines were empty (apparently they had just begun to feed). Finally, all seven that were collected during midday were full of food.

All 11 specimens with material in their stomachs contained only a thick mucus rich in nematocysts, zooxanthellae, and organic debris (mean percent of diet volume and ranking index: 99.8). The balance of the gut contents was made up of diatoms and a few algal fragments.

It is well known that stony corals increase their production of mucus when injured, so this chaetodontid's habit of seeking out abrasions on coral may explain why its gut contents include so much mucus. This species probably obtains significant nourishment from coral mucus, but judging from the numbers of zooxanthellae and

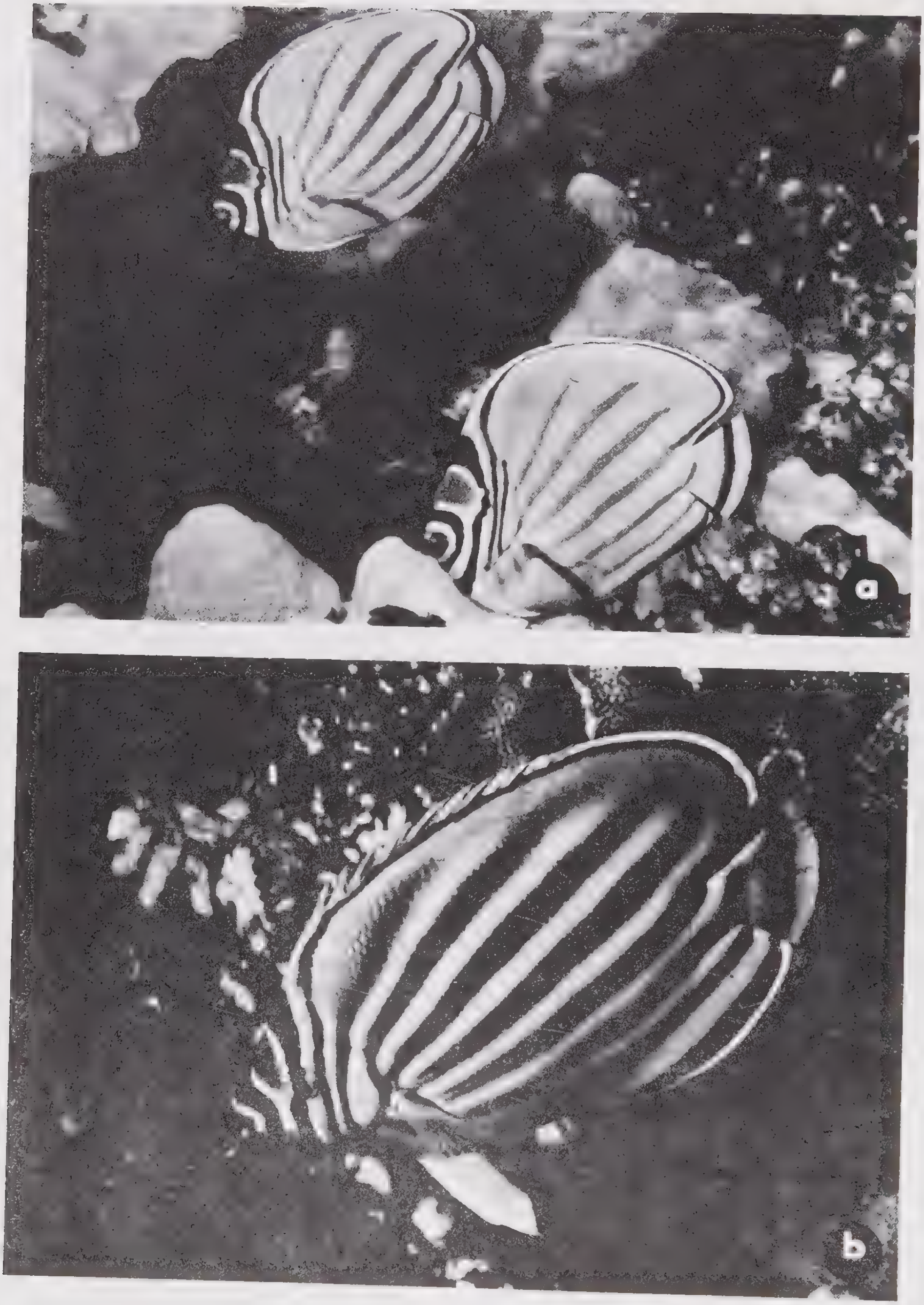


FIGURE 29.—*Chaetodon ornatissimus,* a butterflyfish: a, showing its diurnal coloration while swimming above the reef during the day; b, showing its nocturnal coloration while close to the reef at night.

nematocysts present, at least some coral tissue is also taken (although nothing was found recognizable as such). Presumably at least much of this material had been freshly ingested, because it came from individuals that were actively feeding when collected. Johannes (1967) and Coles and Strathman (in press) have shown there are significant quantities of organic material in coral mucus that could nourish a wide range of animals, including fishes. A similar butterflyfish, *Chaetodon trifasciatus,* not numerous in Kona, has feeding behavior similar to *C. ornatissimus.*

CONCLUSION.—*Chaetodon ornatissimus* is a diurnal fish that feeds on coral during the day, obtaining significant nourishment from coral mucus.

Chaetodon auriga Forskål

In Kona this chaetodontid is less abundant than many of its congeners. Generally paired, it swims close to the reef in daylight, occasionally picking at objects on the sea floor. At night it is alert close among ledges and other reef irregularities.

All six specimens (151: 132-160 mm) collected had full stomachs including four taken during the afternoon and two taken on a dark night, 3 h after sunset. All these specimens contained similar prey in what seemed similar condition. The data are too few to draw conclusions regarding nocturnal activity, but suggest that this species may feed after dark. Items in the stomachs of these six specimens are listed in Table 36.

Most of the food items were fragmented, including the unidentified material, and many of them were relatively fresh. Clearly, this chaetodontid obtains most of its food by tearing pieces from larger sessile organisms. Hiatt and Strasburg (1960) found similar prey in *C. auriga* from the Marshall Islands.

CONCLUSION.—*Chaetodon auriga* preys on a wide variety of benthic organisms during the day, obtaining most of its food by tearing off pieces of larger sessile animals. It also seems to feed to some extent after dark.

Chaetodon fremblii Bennett—blue-striped butterflyfish

This butterflyfish is most numerous where large basalt boulders are interspersed with small pockets of sand. Sometimes paired, but more often solitary, this chaetodonid picks at objects on the rocks and in the sand during the day. At night it occurs close among cover, alert but seemingly inactive.

Fourteen specimens (103: 86-120 mm) were speared during day and night. All eight collected during the afternoon had full stomachs, whereas the two taken from among rocks at night, between 4 and 5 h after sunset, were empty. On the other hand, three others collected together among the rocks during morning twilight, about 25 min before sunrise after a moonless night, had material in their stomachs. Two of them contained only a few well-digested fragments that could have been

TABLE 36.—Food of *Chaetodon auriga.*

Rank	Items	No. fish with this item (*n* = 6)	Mean percent of diet volume	Ranking index
1	Alcyonarians	5	31.0	25.83
2	Terebellid polychaete tentacles	6	18.4	18.40
3	Gastropod egg masses	6	8.8	8.80
4	Errant polychaete fragments	5	5.4	4.50
5	Sabellid polychaete radioles	4	2.2	1.47
6	Echinoid podia	4	2.0	1.33
7	Caridean shrimps	4	1.4	0.93
8	Anemones	1	4.0	0.67
9	Sponges	1	3.1	0.52
10	Sipunculid introverts	3	0.4	0.20
11	Gammaridean amphipods	3	0.4	0.20
12	Hydroids	1	0.2	0.03
13	Serpulid polychaete fragments	1	0.2	0.03
Also,	Unidentified fragments	6	20.7	20.70
	Algal fragments	3	1.8	0.90

taken the previous day, but in the third individual a wide variety of differentially digested items indicated either nocturnal feeding or unusually slow digestion. A fourth individual taken during morning twilight was empty. Items in the eight specimens containing identifiable material, much of it fragments torn from larger sessile animals, are listed in Table 37.

CONCLUSION.—*Chaetodon fremblii* preys on a wide variety of benthic organisms during the day, obtaining much of its food by tearing off pieces of larger sessile animals. With some uncertainty, it seems largely inactive after dark.

Chaetodon lunula (Lacépède)— masked butterflyfish

This butterflyfish, one of the more numerous in Kona, is most abundant where a coral-crested reef face falls among basalt boulders, yet occurs in a variety of habitats. Setting it apart from all other chaetodontids reported here, I never saw this species feed during the day. It generally hovers close to the reef in daylight, sometimes solitary, or in twos or threes, and often in large aggregations (Figure 30). These aggregations form day after day in the same locations, and several occurred in the same places over the entire 15-mo period of the study. The aggregations disperse at nightfall, and after dark the species scatters over the reef, either solitarily, or in twos or threes.

Of the 26 specimens (134: 112-150 mm) examined, all 14 speared at night (more than 4 h after sunset), or during morning twilight, had stomachs full of food in varying stages of digestion, much of it fresh; the other 12 were collected during afternoons (some from the daytime aggregations), and although they too had full stomachs, the contents generally were further digested. There was no recognizable difference in the composition of the diet between specimens collected during each of these three periods. Items in the stomachs are listed in Table 38.

Clearly, *C. lunula,* like *C. auriga* and *C. fremblii,* habitually tears pieces off the bodies of larger sessile animals, but, more so than the others, also takes whole organisms. In fact, its major prey, based on these data, are opisthobranch gastropods, which it takes whole. The opisthobranchs are mostly one form of Anaspidea and one form of Cephalaspidea. Significantly, all individuals of *C. lunula* that contained what seemed to be freshly ingested opisthobranchs were speared at night. Opisthobranchs in *C. lunula* speared during the afternoon were consistently far digested. These opisthobranchs are mostly about 4 to 10 mm long, and are relatively solid pieces of meat that may take longer to digest than many other kinds of food. Similarly, the polychaete heads and prosobranch gastropod heads taken by this fish are relatively dense pieces of meat that probably resist digestion (the shells of the prosobranch gastropods were never present—only the heads, which this butterflyfish apparently is adept at snipping off). Smaller organisms that would be rapidly digested like the amphipods and isopods, generally, but with two exceptions, were absent in specimens speared during the afternoon. Generally then, the stomach contents appeared to have been taken mostly at night. Finally, it may be significant that the eyes of *C. lunula* are relatively larger than the eyes of all other species of this genus studied at Kona.

TABLE 37.—Food of *Chaetodon fremblii.*

Rank	Items	No. fish with this item (*n* = 8)	Mean percent of diet volume	Ranking index
1	Terebellid polychaete tentacles	6	25.0	18.75
2	Sipunculid introverts	6	15.0	11.25
3	Gammaridean amphipods	8	10.1	10.10
4	Errant polychaete fragments	4	3.1	1.55
5	Hydroids	2	2.9	0.73
6	Isopods	3	1.6	0.60
7	Gastropod egg capsules	1	3.6	0.45
8	Caprellid amphipods	1	2.3	0.29
9	Acorn worms	1	2.3	0.29
10	Opisthobranch gastropods	1	1.4	0.18
11	Caridean shrimps	1	0.1	0.01
12	Gastropod opercula	1	0.1	0.01
Also, unidentified fragments		6	21.3	15.98
	Algai fragments	7	11.2	9.80

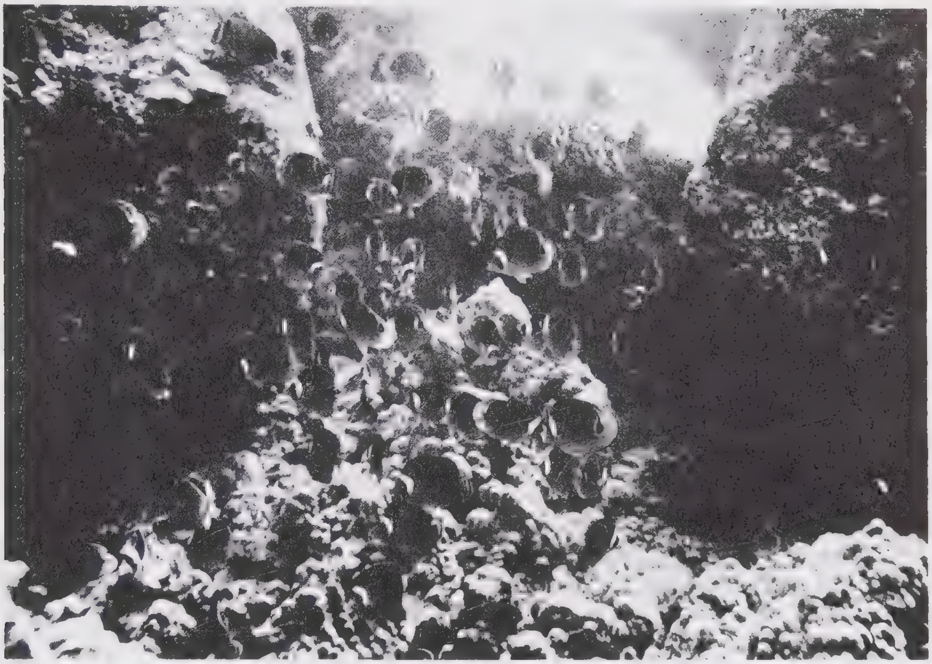


FIGURE 30.—Diurnal aggregation of *Chaetodon lunula*, a butterflyfish.

TABLE 38.—Food of *Chaetodon lunula*.

Rank	Items	No. fish with this item (*n* = 26)	Mean percent of diet volume	Ranking index
1	Opisthobranch gastropods	21	29.2	23.58
2	Terebellid polychaete tentacles	11	8.7	3.68
3	Errant polychaete fragments	17	2.2	1.44
4	Sipunculid introverts	9	1.7	0.59
5	Polychaete heads	8	1.9	0.58
6	Prosobranch gastropod heads	7	0.7	0.19
7	Gammaridean amphipods	9	0.3	0.10
8	Holothurians	2	1.3	0.10
9	Fish eggs	2	1.1	0.08
10	Caridean shrimps	4	0.3	0.05
11	Echinoid podia	4	0.2	0.03
12	Alcyonarians	2	0.3	0.02
13	Sabellid polychaete radioles	3	0.2	0.02
14	Caprellid amphipods	3	0.1	0.01
15	Crustacean eggs	1	0.2	<0.01
16	Tanaids	2	0.1	<0.01
17	Hydroids	2	0.1	<0.01
18	Anemones	1	0.1	<0.01
19	Calanoid copepods	1	0.1	<0.01
20	Crabs	1	0.1	<0.01
21	Tunicates	1	0.1	<0.01
Also,	unidentified fragments	24	50.3	46.43
	Algal fragments	5	0.5	0.10
	Crustacean fragments	4	0.2	0.03

Hiatt and Strasburg (1960) noted only tips of coral polyps in one *C. lunula* from the Marshall Islands. Although the diet of this individual diverges sharply from that of representatives in Kona, one cannot speculate on its significance from one specimen.

CONCLUSION.—*Chaetodon lunula* preys on benthic invertebrates, especially opisthobranchs, at night.

General Remarks on Angelfishes and Butterflyfishes

The two Hawaiian angelfishes, *Holacanthus arcuatus* and *Centropyge potteri,* have feeding habits that set them apart from the butterflyfishes. *Holacanthus arcuatus* is the only chaetodontid that feeds strictly on sponges, and *C. potteri* is the only one that takes just algae and detritus. Thus the Hawaiian situation parallels that in the tropical Atlantic, where species of *Holacanthus* and of *Pomacanthus* (another genus of angelfish) feed mostly on sponges and where species of *Centropyge* feed almost exclusively on algae and detritus (Randall, 1967). Similarly, Hiatt and Strasburg (1960) reported a strictly herbivorous diet for *C. flavissimus* in the Marshall Islands.

Although butterflyfishes in Kona are more strictly predators in the conventional sense than are the angelfishes, Hiatt and Strasburg (1960) reported *Chaetodon reticulatus* in the Marshall Islands to be strictly herbivorous. That species is seen only occasionally in Kona, and so was not included in the present study. Otherwise, Hiatt and Strasburg found scleractinian corals and polychaetes to be the major food of butterflyfishes in the Marshall Islands, and this is in broad accord with the habits of certain species in Kona. Randall (1967) reported that West Indian butterflyfishes feed primarily on anthozoans and the tentacles of polychaetes, again paralleling the habits of certain Kona species. On the other hand, the number of planktivorous butterflyfishes in Kona seems on a scale without parallel in published accounts of other reef areas.

Chaetodontids have been widely described as diurnal fishes, e.g. in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972), and in the Gulf of California (Hobson, 1965, 1968a). Although diurnal habits are generally characteristic of chaetodontids in Kona, the fact that at least one, *Chaetodon lunula,* is nocturnal and that several others feed at least somewhat after dark may reflect increased interspecific pressures associated with the large number of *Chaetodon* species on Kona reefs. I treat the nine most numerous species of *Chaetodon* here, but also saw five others during this study.

Family Pomacentridae: damselfishes

Plectroglyphidodon johnstonianus Fowler and Ball

This solitary species is most numerous where stony corals abound. During the day it swims close to the reef, each individual seemingly associated with a particular location, and here it picks frequently at the substratum, especially around coral. At night it is secreted deep among the coral, relatively inactive, but alert.

Of the eight specimens (60: 39-70 mm) examined, the stomachs of two that were speared among the coral shortly before dawn contained only a few well-digested fragments (probably material that had been ingested during the previous day), whereas the stomachs of all six taken during midday were full of food, much of it fresh.

The major food item in all six was anthozoans: nematocysts and zooxanthellae, with tissue fragments and mucus, but no skeletal material (mean percent of diet volume and ranking index: 94.3). All other items made up only a minor part of the diet: algal fragments in three (mean percent of diet volume: 2; ranking index: 1), sipunculid introverts in one (mean percent of diet volume: 0.2; ranking index: 0.03), and unidentified fragments in four (mean percent of diet volume: 3.5; ranking index: 2.33). Because *P. johnstonianus* is closely associated with scleractinian corals, these probably are the anthozoans so prominent in its diet. However, specific identifications of the fragmented gut contents remain uncertain, and because direct observations of feeding are limited, other anthozoans may also be involved. In any event, the observations indicate that this fish is adept at snipping off pieces of anthozoan tissue and mucus without taking any of the surrounding skeletal material.

CONCLUSION.—*Plectroglyphidodon johnstonianus* is a diurnal predator that feeds chiefly on anthozoans.

Pomacentrus jenkinsi Jordan and Evermann

This species is one of the more widespread and numerous in Kona, especially in relatively quiet water over coral and rocks. During the day, individuals are scattered among reef irregularities, each seemingly associated with specific locations, and here they pick at coral and rock surfaces. At night they hover under cover, remaining alert but relatively inactive until shortly after first light, when diurnal activity is resumed.

Twenty-two specimens (89: 80-100 mm) were collected during day and night. All 12 that were speared as they swam close to the reef during midday were full of food, much of it fresh, whereas of 5 that were speared in reef crevices at night (between 4 and 5 h after last evening light), the stomachs of 3 were empty and those of the other 2 contained only a few well-digested, unidentified fragments. Finally, of five active individuals that were collected during morning twilight and during the first 30 min after sunrise, two were empty, and three contained in their stomachs a few fresh fragments that appeared to have been recently ingested. The 15 specimens that contained at least some fresh material had consumed the items listed in Table 39.

The amorphous organic fragments that constituted the bulk of the gut contents in this fish were in part items that had been digested beyond recognition; however, most of this material appeared to be detritus—organic deposits—that had been scraped from the reef. Gosline and Brock (1960) noted that *P. jenkinsi* inhabits quiet water, where it feeds on algae, and perhaps detritus. Hiatt and Strasburg (1960) also found this fish in quiet water in the Marshall Islands and reported it to be primarily a herbivore that feeds occasionally on small fishes.

CONCLUSION.—*Pomacentrus jenkinsi* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from reef surfaces.

Abudefduf sindonis (Jordan and Evermann)

This damselfish occurs where basalt boulders are swept by a strong surge. Activity is limited to daylight; at night it remains under cover among the rocks.

All five specimens (91: 81-102 mm) were speared during the day, and their guts were full of the material listed in Table 40, much of it fresh. The amorphous organic fragments, the major food item, probably are largely detritus from the reef, such as is also taken by *Pomacentrus jenkinsi*, discussed above. Where a strong surge sweeps the boulder habitat, *A. sindonis* replaces *P. jenkinsi* in depths shallower than about 3 m.

Gosline and Brock (1960) noted that *A. sindonis* seems restricted to surge areas among lava rocks and appears to be omnivorous.

CONCLUSION.—*Abudefduf sindonis* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from the substratum.

Abudefduf sordidus (Forskål)—*kupipi*

Although juveniles of *A. sordidus* are prominent in tide pools, the adults, which are the largest of the Hawaiian pomacentrids, seem to occur only where a precipitous basalt reef face confronts a prevailing swell. In this situation large individuals of this species are fairly numerous among rocky crevices and close to boulders at the base of the reef. Generally a solitary fish, *A. sordidus* is

TABLE 39.—Food of *Pomacentrus jenkinsi*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	15	24.1	24.10
2	Sponges	6	5.7	2.28
3	Calanoid copepods	1	4.6	0.31
4	Errant polychaetes	2	2.0	0.27
5	Fish eggs, demersal	2	1.0	0.13
6	Cyclopoid copepods	4	0.4	0.11
7	Gammaridean amphipods	2	0.2	0.03
8	Barnacle cirri	1	0.1	<0.01
9	Pelecypod mollusks	1	0.1	<0.01
Also, amorphous organic fragments		15	60.1	60.10
	Sand	4	1.7	0.45

TABLE 40.—Food of *Abudefduf sindonis*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	39.4	39.40
2	Polychaetes	4	2.2	1.76
3	Gammaridean amphipods	4	2.2	1.76
4	Caridean shrimps	1	7.0	1.40
5	Cyclopoid copepods	4	1.0	0.80
6	Hydroids	1	1.0	0.20
7	Sipunculid introverts	1	0.2	0.04
8	Insects	1	0.2	0.04
Also, amorphous organic fragments		5	46.8	46.80

TABLE 41.—Food of *Abudefduf sordidus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	35.0	35.00
2	Crabs	4	20.0	16.00
3	Sponges	4	12.2	9.76
4	Prosobranch gastropods	4	9.2	7.36
5	Gammaridean amphipods	5	4.4	4.40
6	Prosobranch gastropod eggs	2	1.2	0.48
7	Tanaids	3	0.6	0.36
8	Hydroids	2	0.4	0.16
9	Bryozoans	2	0.4	0.16
10	Polychaetes	2	0.4	0.16
11	Pycnogonids	2	0.4	0.16
12	Insects	1	0.4	0.08
Also, unidentified fragments		5	15.4	15.40

active only during daylight, close to the substratum. After dark it is secreted under rocky cover, alert but relatively inactive.

All five specimens (147: 129-160 mm) were speared during midday, and their guts were full of the material listed in Table 41, much of it fresh. Gosline and Brock (1960) reported that the young of *A. sordidus* are very prominent tide-pool inhabitants and that the omnivorous adults apparently live just outside of the reef edge.

CONCLUSION.—*Abudefduf sordidus* is a diurnal omnivore that takes chiefly algae and small animals from the substratum.

Abudefduf imparipennis (Sauvage)

This pomacentrid is numerous on shallow, surge-swept reefs where exposed basalt is dotted by the coral *Pocillopora meandrina*. It is a solitary, bright-eyed little fish that is active in daylight, and does not swim away from the substratum. Appearing tense and alert, even when hovering motionless at the base of a coral head, its movements are short but rapid darts from one spot to another. At night it takes shelter deep within reef crevices.

All 15 specimens (42: 29-50 mm) were active on the reef during the day when collected, and all contained food, including fresh material, as listed in Table 42. Gosline and Brock (1960) noted that this fish seems to occur over all rocky areas in the surge zone, and that it appears to be entirely carnivorous, with the predominant food organism being a polychaete annelid.

CONCLUSION.—*Abudefduf imparipennis* is a diurnal predator that feeds mainly on small benthic crustaceans and polychaetes.

Abudefduf abdominalis (Quoy and Gaimard)—*maomao*

This damselfish is most numerous where basalt boulders lie at the base of a vertical reef face in water 5 to 10 m deep. During daylight it hovers in aggregations high in the water column close to the

TABLE 42.—Food of *Abudefduf imparipennis*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	12	12.6	10.08
2	Polychaetes	7	17.6	8.21
3	Cyclopoid copepods	9	7.1	4.26
4	Sipunculid introverts	8	1.9	1.01
5	Fish eggs, demersal	3	3.1	0.62
6	Unidentified eggs, demersal	4	1.8	0.48
7	Opisthobranch gastropods	2	1.7	0.23
8	Diatoms	6	0.5	0.20
9	Algae fragments	2	0.8	0.11
10	Prosobranch gastropod eggs	1	0.8	0.05
11	Isopods	2	0.4	0.05
12	Sponge spicules	1	0.3	0.02
13	Caprellid amphipods	1	<0.1	<0.01
14	Harpacticoid copepods	1	<0.1	<0.01
15	Caridean shrimps	1	<0.1	<0.01
16	Mites	1	<0.1	<0.01
17	Insects	1	<0.1	<0.01
Also, unidentified fragments		15	50.9	50.90

TABLE 43.—Food of *Abudefduf abdominalis*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	54.0	54.00
2	Cyclopoid copepods	8	6.5	5.20
3	Fragments of algae	4	2.6	1.04
4	Fish eggs, planktonic	4	2.0	0.80
5	Polychaetes	4	1.9	0.76
6	Decapod shrimps	4	1.7	0.68
7	Larvaceans	1	4.0	0.40
8	Harpacticoid copepods	4	0.8	0.32
9	Gelatinous clumps of blue-green algae	2	1.3	0.26
10	Pelecypod larvae	2	0.2	0.04
11	Penaeid shrimp larvae	1	0.2	0.02
12	Gastropod veligers	1	0.1	0.01
13	Naupilius larvae	1	0.1	0.01
Also, unidentified fragments		9	24.6	22.14

reef, where it picks organisms from the plankton. Although members of an aggregation are close to one another, each feeds independently. The plankters are taken with what seems to be a visually directed action in which the fish suddenly thrusts both jaws forward, then immediately retracts them. Presumably the sudden expansion of the oral cavity sucks the prey in.

A given aggregation maintains station over a particular location although its position in the water column is influenced by several factors. Fish size is important, because the larger individuals tend to be farther above the reef than the smaller ones. Prevailing light is another factor; thus, when clouds pass in front of the sun, and light diminishes, individuals of all sizes descend closer to the reef. In addition, the appearance of a large predator, or some other disturbance, intermittently sends this fish diving to cover on the reef. However, after such an event it quickly returns to its feeding stations in the water column.

As light progressively fades late in the day, this species gradually descends to the reef so that by evening twilight it is sheltered among the coral (Hobson, 1972). On dark nights it remains under cover, relatively inactive but alert; however, under bright moonlight it swims in exposed positions close to the reef. Then, during morning twilight, it begins to ascend to its daytime feeding stations in the water column (Hobson, 1972).

Of 14 specimens (142: 105-162 mm) examined, the 4 that were speared as they hovered among the rocks on dark nights (between 4 and 6 h after sunset) contained only well-digested fragments, whereas all 10 that were speared from mid-water aggregations during afternoons had their stomach full of food (including much fresh material), as listed in Table 43.

CONCLUSION.—*Abudefduf abdominalis* is a diurnal planktivore that preys primarily on copepods.

Dascyllus albisella Gill

Where corals are abundant, this damselfish is numerous to depths of at least 35 m. During daylight, it aggregates in the water column and picks small organisms from the plankton, much as does *Abudefduf abdominalis,* described above, and its aggregations rise and fall in the water column in response to the same variables that influence that species. Also like *A. abdominalis, D. albisella* descends to the reef during evening twilight and spends the night close among the rocks—under cover on dark nights, and in exposed positions when there is moonlight.

Twelve specimens (79: 42-95 mm) were collected during day and night. The six that were speared shortly before first morning light as they hovered among the coral contained only a few well-digested fragments (five were taken after nights of bright moonlight, one after a dark night). On the other hand, the six that were collected from aggregations in the water column during afternoons had stomachs full of food, including much fresh material as listed in Table 44.

Gosline and Brock (1960) reported that *D. albisella* occurs in small schools around certain large coral heads and listed stomach contents as follows: shrimp and crab larvae, mysids, and calanoid copepods.

CONCLUSION.—*Dascyllus albisella* is a diurnal planktivore that takes primarily larvaceans and copepods.

Chromis vanderbilti (Fowler)

This, the smallest pomacentrid in Kona, is numerous where exposed basalt ledges are interspersed with coral. During the day it aggregates in the water column, but even under bright sunlight rarely moves more than 50 cm above the reef. On overcast days it generally remains sheltered, and shortly before sunset is the first planktivorous damselfish to descend to cover on the reef (Hobson, 1972). At night, it usually remains out of sight deep within reef crevices, and in the morning is the last pomacentrid to appear.

All 12 specimens (38: 17-46 mm) taken from feeding aggregations during midday had stomachs full of food, including fresh material, as listed in Table 45.

CONCLUSION.—*Chromis vanderbilti* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis leucurus Gilbert

Gosline and Brock (1960) considered *C. leucurus* to include two distinct color phases: in one the body is very dark anteriorly and abruptly white posteriorly; in the other, the whole body, except black pectoral base and white caudal fin, is mostly plain orange-brown. Although I followed this judgment when making the fish counts, the probability that at least two species are represented, and that neither one may in fact be *C. leucurus,* is currently under study by John E. Randall, B. P. Bishop Museum, and Stanley Swerdloff, Government of American Samoa. In any event, the specimens collected for study of food

TABLE 44.—Food of *Dascyllus albisella*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Larvaceans	6	43.1	43.10
2	Calanoid copepods	6	11.2	11.20
3	Cyclopoid copepods	6	9.2	9.20
4	Gelatinous clumps of blue-green algae	4	7.2	4.80
5	Fragments of algae	4	1.5	1.00
6	Decapod shrimp larvae	2	2.2	0.73
7	Fish eggs, planktonic	2	1.1	0.37
8	Hydroid fragments	1	0.2	0.03
9	Pelecypod larvae	1	0.2	0.03
10	Gammaridean amphipods	1	0.2	0.03
11	Harpacticoid copepods	1	0.2	0.03
Also, unidentified fragments		5	23.7	19.75

TABLE 45.—Food of *Chromis vanderbilti*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	30.5	27.96
2	Larvaceans	8	21.7	14.47
3	Cyclopoid copepods	12	8.8	8.80
4	Polychaetes	5	0.9	0.38
5	Fish eggs, planktonic	4	0.9	0.30
6	Decapod shrimps	2	1.7	0.28
7	Harpacticoid copepods	3	1.1	0.28
8	Siphonophores	1	1.7	0.14
9	Gelatinous clumps of blue-green algae	2	0.5	0.08
10	Ostracods	1	0.5	0.04
11	Hyperiid amphipods	1	0.1	0.01
Also, unidentified fragments		12	31.1	31.10

habits, below, all represent the orange-brown form.

Of the two, the orange-brown form is the more numerous in Kona, but both abound over coral-rich reefs, often together in plankton-feeding aggregations that hover within 1 m of the substratum during the day. As is true of *Abudefduf abdominalis* and *Dascyllus albisella*, described above, *C. leucurus* remains closer to the reef when light is diminished, and dives to cover when threatened (Figure 31). At night it generally is out of sight within crevices.

All five specimens (57: 37-70 mm) speared during midday had their stomachs full of food, including fresh material, as listed in Table 46.

Swerdloff (1970a) described the behavior of two spatially related species of *Chromis* in the Marshall Islands, *C. leucurus*, and *C. dimidiatus*, and reported their food to be calanoid copepods, fish eggs, and larval tunicates.

CONCLUSION.—*Chromis leucurus* is a diurnal planktivore that takes primarily copepods and larvaceans.

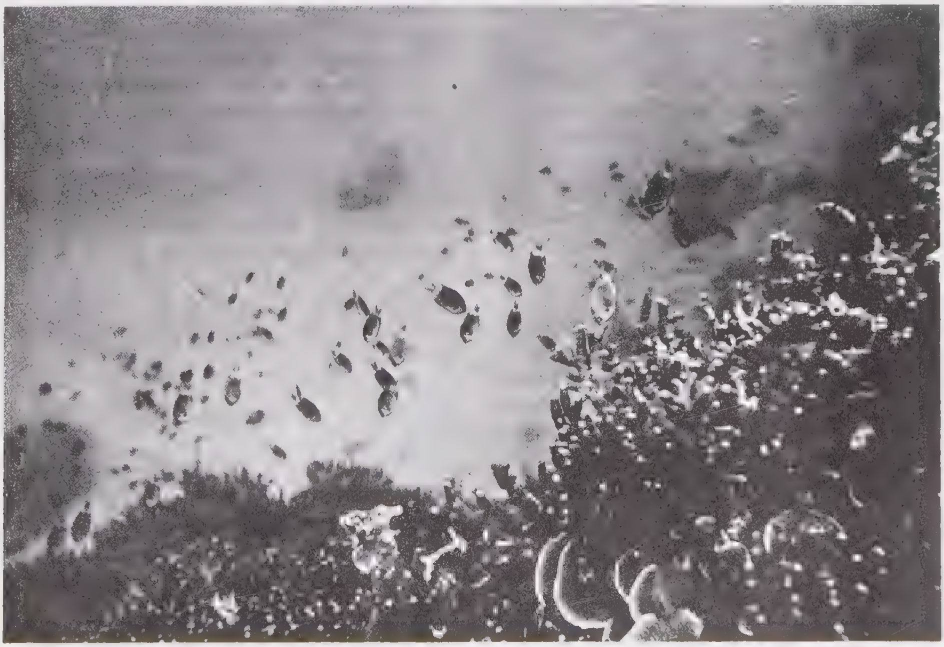


FIGURE 31.—Members of an aggregation of *Chromis leucurus*, a damselfish, having been threatened, dive from their plankton-feeding location in the water column toward shelter among the coral below.

TABLE 46.—Food of *Chromis leucurus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Cyclopoid copepods	5	19.0	19.00
2	Larvaceans	3	22.0	13.20
3	Calanoid copepods	3	4.0	2.40
4	Fish eggs, planktonic	4	2.8	2.24
5	Gelatinous clumps of blue-green algae	3	3.6	2.16
6	Fragments of algae	2	2.0	0.80
7	Harpacticoid copepods	1	0.4	0.08
Also, unidentified fragments		5	46.2	46.20

TABLE 47.—Food of *Chromis verater*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	5	29.6	29.60
2	Larvaceans	4	36.0	28.80
3	Cyclopoid copepods	5	2.2	2.20
4	Fish eggs, planktonic	3	2.4	1.44
5	Decapod shrimps	1	7.0	1.40
6	Siphonophores	1	0.8	0.16
7	Mysids	1	0.4	0.08
8	Chaetognaths	1	0.4	0.08
9	Polychaetes	1	0.2	0.04
10	Harpacticoid copepods	1	0.2	0.04
Also, unidentified fragments		5	20.8	20.80

Chromis verater Jordan and Metz

This damselfish is one of the more prominent fishes over both coral and basalt reefs in Kona at depths below about 15 m. During the day it swims in plankton-feeding aggregations that hover 2 to 5 m above the reef, where changing light levels and the appearance of certain predators produce effects much as described above for *Abudefduf abdominalis* and other planktivorous pomacentrids. Also as in these other species, *C. verater* passes the night among cover on the reef, relatively quiet but alert. It moves about under moonlight, but rests in crevices on dark nights.

Of the seven specimens (120: 100-141 mm) examined, two that were collected from among cover on the reef shortly before first morning light (one after a night of bright moonlight, the other after a dark night) contained only a few well-digested fragments, whereas, all five speared from aggregations above the reef during afternoons were full of food (including fresh material), as listed in Table 47.

Swerdloff (1970b), who recognized that *C. verater* inhabits relatively deep water, reported the following categories of prey in 13 specimens from one collection on the island of Oahu (ranked as percent of the diet): copepods, 71.5%; tunicates, 17.6%; malacostracans, 4.7%; mollusks, 2.5%; fish eggs, 1.7%; and siphonophores, 1.7%. He also presented additional data of food habits, as he compared the ecology of *C. verater* with that of its congener *C. ovalis* see below).

Gosline and Brock (1960) noted that *C. verater* occurs in deeper water than other Hawaiian pomacentrids. This conclusion was later supported by Brock and Chamberlain (1968) who, making observations from a submarine, found *C. verater* to be the most abundant reef fish around rocky outcrops at a depth of 70 m.

CONCLUSION.—*Chromis verater* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis ovalis (Steindachner)

This species is less numerous in Kona than any of the other planktivorous damselfishes described above. It occurs over irregular substrata of exposed basalt interspersed with coral at depths between 5 and 20 m. During the day it aggregates 2 to 5 m above the reef—at about the same level as *C. verater*, with which it often forms mixed groups (Swerdloff, 1970b). Its reactions to changing light and threatening situations are as described above

TABLE 48.—Food of *Chromis ovalis*.

Rank	Items	No. fish with this item (n = 2)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	2	47.5	47.50
2	Larvaceans	2	7.5	7.50
3	Cyclopoid copepods	2	3.0	3.00
4	Mysids	1	2.5	1.25
5	Decapod shrimps	1	2.5	1.25
Also, unidentified fragments		2	37.0	37.00

for *Abudefduf abdominalis* and for other planktivorous pomacentrids; its nocturnal behavior also is like that described for these other species.

Of six specimens (124: 121-138 mm) examined, all four that were speared among corals shortly before first morning light (two after dark nights, two after moonlit nights) contained only a few well-digested fragments, whereas two that were speared from aggregations above the reef during midafternoon were full of food (including fresh items), as listed in Table 48.

Swerdloff (1970b) reported the following categories of prey in eight *C. ovalis* from one collection on the island of Oahu (ranked as percent of the diet): copepods, 60.1%; tunicates, 16.9%; malacostracans, 9.5%; mollusks, 9.5%; polychaetes, 2.3%; fish eggs, 0.8%; and siphonophores, 0.8%. Gosline and Brock (1960) reported "a mass of copepods" in the stomach of one individual of this species.

CONCLUSION.—*Chromis ovalis* is a diurnal planktivore that takes primarily copepods.

General Remarks on Damselfishes

Pomacentrids are widely recognized as being active by day and relatively inactive at night. For example, they were so described in the Gulf of California (Hobson, 1965, 1968a), and also in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972). Food-habit data from the various members of this family in areas as widely separated as the West Indies (Randall, 1967) and the Marshall Islands (Hiatt and Strasburg, 1960) show widely divergent habits: some are strictly herbivorous, others are omnivorous, and still others are strictly carnivorous.

The habitat of each pomacentrid in Kona is especially well defined. Two major categories exist: those that forage on the bottom and those that feed in the water column.

BOTTOM FEEDERS.—Pomacentrids that forage on the sea floor have especially diverse diets. Algae and organic detritus are the major foods of many, especially among species of *Pomacentrus* (Hiatt and Strasburg, 1960; Randall, 1967). In Kona, *P. jenkinsi* is in this category, but *P. pavo* in the Marshall Islands is primarily a predator on small fishes and crustaceans (Hiatt and Strasburg, 1960). The diets of species of *Abudefduf* appear even more diverse. *Abudefduf sindonis* in Kona has food habits similar to those of *P. jenkinsi,* but the highly omnivorous *A. sordidus* forages on a wide variety of benthic animals and plants, whereas the predaceous *A. imparipennis* takes mostly benthic crustaceans and polychaetes. *Abudefduf saxatilus* in the West Indies is, according to Randall (1967), "one of the most diversified of all fishes in its food habits," feeding as it does on a wide assortment of plants and animals from both sea floor and water column. Similarly, *A. troschelii* in the Gulf of California feeds on zooplankton and bits of algae from the water column, as well as organisms from the substratum (Hobson, 1968a).

WATER-COLUMN FEEDERS.—Planktivorous pomacentrids are prominent on coral reefs throughout tropical seas. Their characteristic mid-water aggregations have been described in the Indian Ocean (Eibl-Eibesfeldt, 1962), central Pacific (Hiatt and Strasburg, 1960), Gulf of California (Hobson, 1965, 1968a), and the tropical Atlantic (Starck and Davis, 1966). In the Bahamas, Stevenson (1972) showed that the height in the water column at which *Eupomacentrus partitus* feeds on plankton is determined largely by light and current. The progressive ascent of planktivorous pomacentrids into the water column during morning twilight, as they rise to their mid-water feeding grounds, and their subsequent descent to the reef during evening twilight, has been described in Kona (Hobson,

1972) and the West Indies (Collette and Talbot, 1972).

Some of these planktivorous pomacentrids, for example *Abudefduf saxatilus* and *A. troschelii,* noted above, also forage part time on the sea floor. However, most of them, including the species of *Chromis* and *Dascyllus,* are specialized as predators on zooplankton, especially copepods. Examples include the representatives of these genera on Kona reefs, described in the present report, as well as others from the central Pacific (Hiatt and Strasburg, 1960) and tropical Atlantic (Randall, 1967).

Family Cirrhitidae: hawkfishes

Paracirrhites arcatus (Cuvier)—*pili ko'a*

This hawkfish is numerous in areas richly overgrown by the coral *Pocillopora meandrina.* Typically, it rests immobile on the coral heads during day, and takes shelter among the coral branches at night. Individuals shorter than about 50 mm are among the coral branches day and night, whereas those longer than about 90 mm frequently occur on the other hard substrata—perhaps because they are too large to fit between the branches of most *Pocillopora* heads. *Paracirrhites arcatus* moves only infrequently—a short dash to capture prey, or when threatened.

Forty-five specimens (82: 49-101 mm) were collected during day and night. The nighttime situation is reflected in the 17 that were speared during the 2 h before first morning light (13 on moonlit nights, 4 on dark nights). Of these, 16 (52 to 95 mm) were resting among branches of *Pocillopora,* whereas the other (99 mm) was amid a fingerlike growth of *Porites compressus.* The stomachs were empty in 13 and contained only well-digested fragments in 3. The last individual, taken during new moon, contained a caridean shrimp that probably had been captured that night.

The daytime situation is reflected in the 12 individuals speared during afternoons, all perched in exposed positions on the reef when collected. Ten of these (71 to 101 mm) rested on *Pocillopora,* and two (95 and 97 mm) rested on rocks. Ten had stomachs full of food, much of it fresh, and although the remaining two had empty stomachs, their intestines were full.

Specimens collected at other times of day and night offer less conclusive data. Of nine speared at night (between 3 and 5 h after sunset), seven were deep among coral branches, but two rested in exposed positions (the latter situation was only rarely seen). Six of these had food in their stomachs, but although the material was well-digested in five, the sixth was full of a species of cyclopoid copepod that often swarmed around our diving lights for about 30 min, an hour or so after last evening light. Finally, of the seven speared within 2 h after sunrise as they rested on top of *Pocillopora* heads, four had the stomachs empty and three contained fresh prey. Identifiable material occurred in 20 of the 46 specimens examined, as listed in Table 49.

Hiatt and Strasburg (1960), reporting on this species from the Marshall Islands, remarked that it habitually lies motionless on the upper surface of living coral heads and listed a diet of crustaceans and fishes.

CONCLUSION.—*Paracirrhites arcatus* is a diurnal predator that feeds primarily on xanthid crabs and other benthic crustaceans.

Paracirrhites forsteri (Bloch and Schneider)—*hilu pili ko'a*

This hawkfish is numerous in coral-rich areas, where it rests immobile in exposed positions on the reef during the day (Figure 32). Its attitude is

TABLE 49.—Food of *Paracirrhites arcatus.*

Rank	Items	No. fish with this item (n = 20)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	43.3	25.98
2	Decapod shrimps	6	15.5	4.65
3	Fish	3	10.5	1.58
4	Ophiuroids	1	5.0	0.25
5	Calapid crabs	1	4.3	0.22
6	Cyclopoid copepods	1	4.0	0.20
7	Crab megalops	2	1.8	0.18
8	Gammaridean amphipods	2	0.5	0.05
9	Calanoid copepods	1	0.3	0.02
Also, crustacean fragments		6	13.5	4.05
	Unidentified fragments	1	1.3	0.07

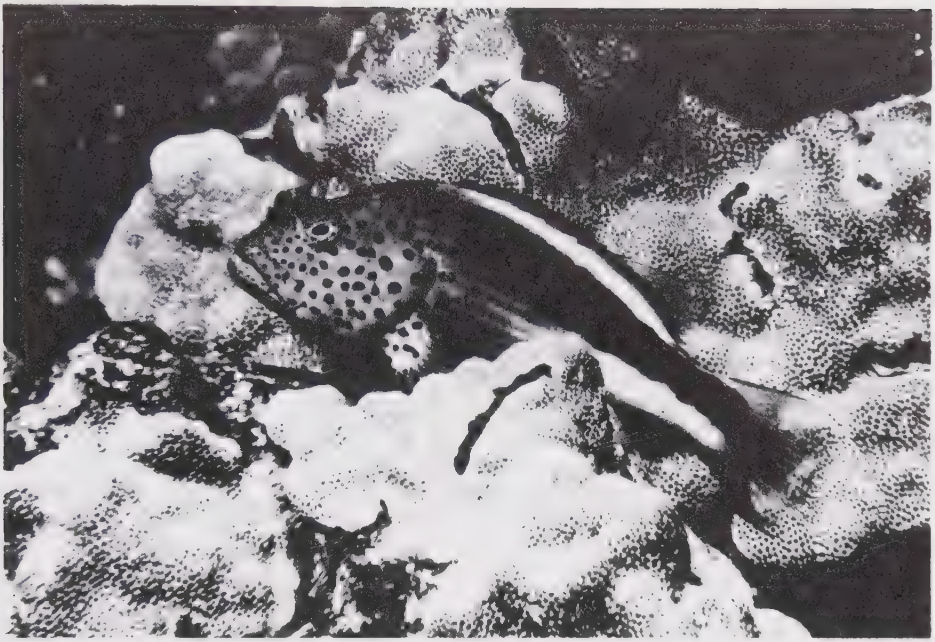


FIGURE 32.—*Paracirrhites forsteri,* a hawkfish, seated on the reef during the day.

much like that of *P. arcatus,* above, but it occurs widely on different hard surfaces, rather than being mostly associated, as is *P. arcatus,* with one type of coral. In the manner typical of hawkfishes, *P. forsteri* moves only infrequently, attacking prey that have come within range of a short, explosive dash. Such attacks were seen only during the day; at night *P. forsteri* generally is out of sight in reef crevices.

Thirty-six specimens (139: 93-181 mm) were collected during day and night. Of the 28 that were speared as they rested during midday on a variety of reef substrata, 18 contained food in the stomach, much of it relatively fresh (although in 1 the material was reduced to unidentifiable fragments). In contrast, among eight others that were speared from deep within reef crevices during the 2 h immediately before first morning light, four had empty stomachs and three contained only well-digested fragments; only the eighth specimen contained relatively fresh prey—a shrimp, *Saron marmoratus*—that appeared to have been taken that night.

Fish were the major prey, occurring in 14 of the 21 individuals that contained identifiable material (mean percent of diet volume: 66.6; ranking index: 44.4). Other food items were: caridean shrimps in four (mean percent of diet volume: 16.2; ranking index: 3.09), xanthid crabs in one (mean percent of diet volume: 4.8; ranking index: 0.23), and unidentified crustacean fragments in three (mean percent of diet volume: 12.4; ranking index: 1.77). The only identifiable fish among the gut contents was a wrasse, *Thalassoma duperrey.* Three of the four individuals containing caridean shrimps had preyed on *Saron marmoratus.* Of the larger shrimps (to about 50 mm), this was the one most frequently seen after dark, but only one of these, noted above, appeared to have been captured at night. Perhaps significantly, the specimens of *P. forsteri* that were examined had preyed on either fishes or crustaceans, but never on both.

Hiatt and Strasburg (1960), citing the similarity in habits between *P. forsteri* and *P. arcatus,* noted that the diet of *P. forsteri* runs more to fishes than crustaceans. I agree with them that this difference probably relates to the size difference between these two congeners.

CONCLUSION.—*Paracirrhites forsteri* is a diurnal predator that preys mostly on small fishes.

Cirrhitops fasciatus (Bennett) — *'o'opu kaha 'iha 'i*

This hawkfish is numerous on both coral and basalt reefs, and unlike the two species of *Paracirrhites,* above, occurs in exposed positions at night as well as during the day. In typical hawkfish fashion, it generally rests immobile on the substratum, except when attacking prey; thus, it is difficult to differentiate periods of activity from periods of inactivity.

Twenty-three specimens (76: 39-91 mm) were collected during night and day. Seven of nine speared from exposed positions under moonlight between 4 and 5 h after sunset contained prey that appeared to have been recently ingested. In addition, three of six individuals taken during the hour immediately before first morning light also contained relatively fresh prey. The daytime situation is reflected by specimens that were collected during afternoons, where the stomachs from six of eight individuals contained prey, much of it relatively fresh. Items in the 16 specimens containing identifiable prey are listed in Table 50.

CONCLUSION.—*Cirrhitops fasciatus* regularly feeds during both day and night, mostly on xanthid crabs and other benthic crustaceans.

Cirrhitus pinnulatus (Bloch and Schneider)— *po'o pa'a*

This hawkfish is numerous at depths of less than 5 m in and around crevices on surge-swept basalt reefs (Figure 5). Corals in this habitat are mostly isolated heads of *Pocillopora meandrina* and encrusting patches of *Porites compressus.* As do other hawkfishes, *C. pinnulatus* generally rests motionless on the substratum. During the day it usually remains under at least partial cover; at night it more frequently occurs in exposed positions on the reef.

All 32 specimens (152: 103-221 mm) that were examined were resting immobile on the reef when speared, most of them partially concealed in crevices. Of 17 taken during the afternoon, 14 had empty stomachs, and 3 contained material extensively damaged by digestion. In contrast, of 15 that were taken between 1 h before first morning light and 2 h after sunrise, only 4 had empty stomachs, whereas each of the other 11 had the stomach full of food, much of it fresh. Items in the 14 individuals containing identifiable material are listed in Table 51.

Most of the xanthid crabs among these gut contents were *Trapezia,* a genus common among branches of the coral *Pocillopora.* Hiatt and Strasburg (1960) also reported a crab of this genus in one *C. pinnulatus* that they examined from the

TABLE 50.—Food of *Cirrhitops fasciatus.*

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	30.9	13.52
2	Decapod shrimps	5	20.9	6.53
3	Crab megalops	2	7.8	0.98
4	Ophiuroids	1	6.3	0.39
5	Octopods	1	6.3	0.39
6	Gammaridean amphipods	1	0.6	0.04
Also, crustacean fragments		5	22.2	6.94
	Unidentified fragments	1	5.0	0.31

TABLE 51.—Food of *Cirrhitus pinnulatus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	11	60.0	47.14
2	Oxyrhynchan crabs	3	7.5	1.61
3	Decapod shrimps	3	2.9	0.62
4	Ophiuroids	1	7.1	0.51
5	Octopods	1	7.1	0.51
6	Echinoids	1	3.2	0.23
7	Pagurid crabs	1	1.1	0.08
Also, crustacean fragments		3	11.1	2.38

Marshall Islands. Randall (1955) reported only brachyuran crabs in the diet of two specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Cirrhitus pinnulatus* is a nocturnal predator that hunts mostly xanthid crabs.

Family Labridae: wrasses

Bodianus bilunulatus (Lacépède) — *'a'awa*

This relatively large, solitary wrasse occurs only infrequently on the shallow reefs in Kona as it lives mostly at depths below 15 m. Two individuals (172 and 283 mm) were speared during midafternoon as they moved actively among coral at 25 m along the outer drop-off, and the guts of both were full of crushed mollusks.

CONCLUSION.—***Bodianus bilunulatus*** feeds on mollusks during the day.

Cheilinus rhodochrous Günther—*po'ou*

This labrid is numerous over both coral and rocky substrata deeper than about 10 m. It is a solitary species that hovers close to the reef during the day and takes shelter in the reef at night. Several times larger individuals attempted to take fish that were impaled on my spear, and twice they succeeded despite my attempts to drive them away.

Among 16 specimens (175: 129-242 mm) collected during afternoons, 6 contained only a few well-digested fragments posteriorly in the gut, and most of the material in the other 10 was far digested. Fish were the major prey, occurring in 4 of the 10 individuals that contained identifiable material (mean percent of diet volume: 40; ranking index: 16). Other food items were: decapod shrimps in three (mean percent of diet volume: 30; ranking index: 9), brachyuran crabs in one (mean percent of diet volume: 8; ranking index: 0.8), unidentified crustacean fragments in two (mean percent of diet volume: 12; ranking index: 2.4), and other unidentified fragments in two (mean percent of diet volume: 10; ranking index: 2). The only fish that could be identified was a pomacentrid, *Pomacentrus jenkinsi*, and the only identifiable shrimp was *Saron marmoratus*. Generally *C. rhodochrous* preys on large organisms, but because it crushes them upon ingestion, identifications are difficult. Presumably crushing the food items accelerates digestion, thus contributing to the poor condition of this material. However, because all these specimens were collected during afternoons, the advanced digestion could also reflect early morning feeding.

Cheilinus rhodochrous is a stalking predator, equipped by a relatively large mouth and pair of large canine teeth at the front of each jaw to hunt prey that are relatively larger and more active than those taken by most other labrids. Most of the specimens that were examined contained a single large prey organism, indicating that feeding is infrequent and that each successful attack provides enough nourishment to sustain the predator for some time.

CONCLUSION.—*Cheilinus rhodochrous* is a diurnal predator that stalks relatively large fishes and crustaceans. It may have peaks in feeding early and late in the day, but is inactive at night.

Pseudocheilinus octotaenia Jenkins

This small species is one of the more numerous labrids on coral-rich reefs at depths to at least 30 m, but its large numbers are difficult to appreciate because it occurs close among the many narrow interstices of the reef. It is strictly a diurnal species that takes shelter in the reef at night.

All 12 specimens (77: 50-95 mm) taken during afternoons had material in their stomachs, but the food items were difficult to identify because they were small and had been crushed when ingested. Thus, most of the gut contents of all 10 individuals that contained recognizable material can be listed only as unidentified crustacean fragments (mean percent of diet volume and ranking index: 71.9). Items that could be identified are: brachyuran crabs in three (mean percent of diet volume: 22; ranking index: 6.6), echinoids in one (mean percent of diet volume: 5; ranking index: 0.5), demersal fish eggs in one (mean percent of diet volume: 1; ranking index: 0.1), and copepods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

CONCLUSION.—*Pseudocheilinus octotaenia* is a diurnal predator that feeds mostly on brachyuran crabs and other benthic crustaceans.

Labroides phthirophagus Randall

This small wrasse (most are less than 100 mm long) is specialized to pick ectoparasites from the bodies of other fishes at well-defined cleaning stations (Figure 33). Usually two or several of these cleaners are active at each station. It is a diurnal species that shelters in reef crevices at night (Hobson, 1972).

This is the major cleaner fish on Hawaiian reefs, and its habits are well known (e.g. Randall, 1958; Youngbluth, 1968; Losey, 1971; Hobson, 1971). Because the activity of this species has been extensively documented, it was only incidentally observed during the present study.

CONCLUSION.—*Labroides phthirophagus* cleans ectoparasites from the bodies of other fishes during the day.

Thalassoma duperrey (Quoy and Gaimard) — *hinalea lauwili*

This is probably the most ubiquitous fish on Kona reefs (Figure 33): it is numerous everywhere, from the surge-swept reef tops to the outer drop-off on both coral-rich and exposed basalt substrata. In the daytime fish counts along transect lines, *T. duperrey* ranked among the five most numerous species in all the sampled habitats. An opportunist, it is consistently the first fish to appear when a sea urchin has been crushed, or when a rock has been overturned and vulnerable organisms exposed. Sometimes it follows close to the feeding jaws of scarids to snap up prey uncovered when these herbivores disturb the substratum. This wrasse is adapted to a wide range of habits: it forages in the water column when plankton are abundant, but mostly picks organisms off a variety of substrata. It is strictly a diurnal species that shelters in reef crevices at night (Hobson, 1972).

Many of the juveniles are cleaners and maintain stations at certain prominent coral heads. On one survey 5 m deep along approximately 1 km of the north shore of Honaunau Bay, I found a cleaning station maintained by these fish at every large head of *Porites pukoensis* that was of a distinctive mustardlike hue and characterized by golf-ball-sized nodules separated by narrow, shallow depressions. The general extent of this cleaner's relationship to this type of coral was not determined, but I saw cleaning stations nowhere else during the survey. Because the juveniles of *T. duperrey* always discontinued cleaning when a human was near, incidental observations of this activity were rare. And, as noted above in discussing *Labroides*

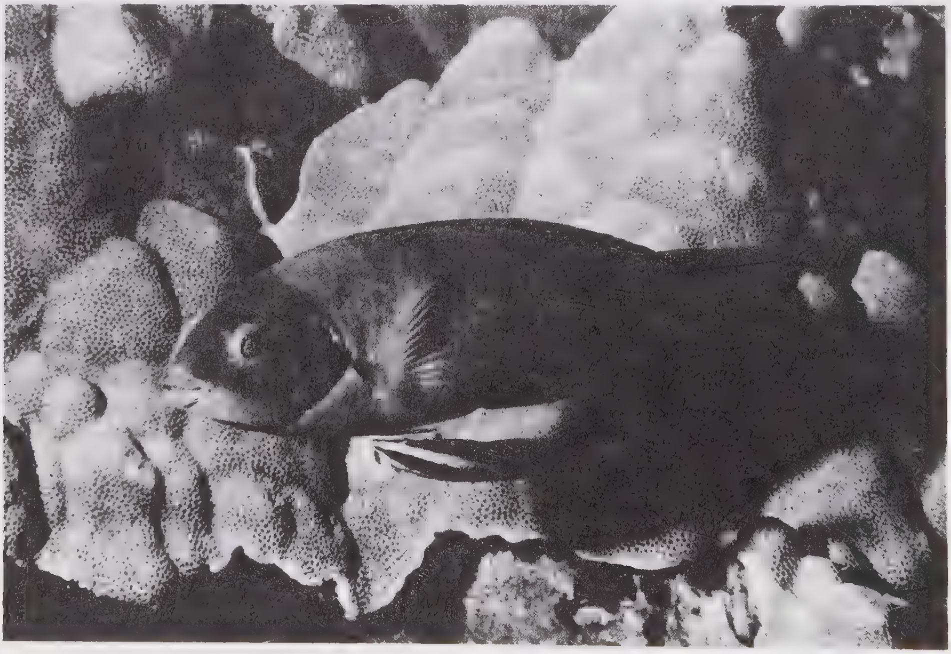


FIGURE 33.—A wrasse, *Thalassoma duperrey*, being cleaned by another wrasse, *Labroides phthirophagus*.

phthirophagus, my observations of cleaning were mostly incidental. Nevertheless, it was evident that cleaning by *T. duperrey* is mostly an activity of juveniles. Adults clean only infrequently, and not at well-defined cleaning stations.

To indicate the food of the post juveniles of this species, 24 specimens, 125 (103-146) mm long, were speared during the day as they swam actively over the reef. All contained identifiable items, as listed in Table 52. In contrast with the diet of most fishes examined during this study, no single item or certain few items predominate in the diet of *T. duperrey*, a circumstance that undoubtedly relates to its populating a wide range of habitats.

CONCLUSION.—*Thalassoma duperrey* is a diurnal predator that feeds on a very wide range of shelled organisms, most of them benthic.

Thalassoma fuscus (Lacépède)—*hou*

This species was shown by numerous observations of spawning aggregations to include the nominal *T. umbrostigma* (which represents the juveniles and females). It is a fish of shallow water along rocky, surge-swept shores and is one of the most numerous species on the shallow reef flats. Generally it does not occur in water deeper than about 5 m and is strictly a diurnal fish that shelters in reef crevices after dark.

All 14 specimens (132: 60-200 mm) speared as they swam on the reef during daylight contained identifiable food material, as listed in Table 53. Hiatt and Strasburg (1960) reported on two specimens of this species (as *T. umbrostigma)* in the Marshall Islands: one had consumed a stomatopod, the other a fish. Randall (1955) reported (also as *T. umbrostigma*) that one specimen taken in the Gilbert Islands contained a crab.

CONCLUSION.—*Thalassoma fuscus* is a diurnal predator that feeds mostly on crabs and mollusks.

Halichoeres ornatissimus (Garrett)—*la'o*

In Kona this labrid is nowhere particularly numerous, yet it occurs regularly in all inshore habitats. It is generally solitary and swims close to cover during the day. At night it is out of sight, presumably resting in crevices or under the sand.

All 13 specimens (96: 76-115 mm), speared during daylight, had a full gut that included fresh material, as listed in Table 54. Food items more than about 4 mm in greatest dimension were crushed, and this included most of the mollusks. Probably at least much of the unidentified material constituted fragmented molluscan soft parts. This fish plucks small benthic organisms off the substratum, including some forms, like the didemnid tunicates, that are attached to the reef.

TABLE 52.—Food of *Thalassoma duperrey*.

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Gastropod mollusks	9	7.5	2.81
2	Echinoids	3	7.9	0.99
3	Brachyuran crabs	3	6.1	0.76
4	Pelecypod mollusks	3	5.0	0.63
5	Gammaridean amphipods	9	1.5	0.56
6	Calanoid copepods	2	6.3	0.53
7	Tanaids	6	1.3	0.33
8	Cyclopoid copepods	4	1.4	0.23
9	Scleractinian corals	2	2.5	0.21
10	Polychaetes	2	2.1	0.18
11	Ophiuroids	2	1.5	0.13
12	Tunicates	2	1.5	0.13
13	Isopods	2	0.9	0.08
14	Fish eggs	2	0.6	0.05
15	Caprellid amphipods	2	0.4	0.03
16	Pagurid crabs	2	0.4	0.03
17	Foraminiferans	1	0.2	<0.01
18	Sipunculid introverts	1	0.2	<0.01
19	Fish	1	0.2	<0.01
20	Unidentified eggs	1	<0.1	<0.01
Also,	crustacean fragments	11	9.4	4.31
	Algae fragments	8	11.5	3.83
	Unidentified material	15	31.5	19.69

TABLE 53.—Food of *Thalassoma fuscus*.

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Brachyuran crabs	7	35.5	17.75
2	Mollusks	5	17.2	6.14
3	Octopods	1	7.1	0.51
4	Ophiuroids	1	5.0	0.36
5	Polychaetes	2	1.8	0.26
6	Sipunculid introverts	2	1.4	0.20
7	Crab megalops	1	2.8	0.20
8	Fish	1	2.5	0.18
9	Gammaridean amphipods	3	0.7	0.15
10	Cyclopoid copepods	3	0.6	0.13
11	Calanoid copepods	1	1.4	0.10
12	Isopods	1	0.1	<0.01
Also,	crustacean fragments	2	3.7	0.53
	Unidentified fragments	8	20.2	11.54

TABLE 54.—Food of *Halichoeres ornatissimus*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Mollusks	6	13.5	6.23
2	Gammaridean amphipods	7	7.7	4.15
3	Colonial diatoms	4	6.9	2.12
4	Didemnid tunicates	3	8.8	2.03
5	Tanaids	5	1.5	0.58
6	Harpacticoid copepods	4	1.7	0.52
7	Sipunculid introverts	3	1.2	0.28
8	Ophiuroids	1	3.1	0.24
9	Cyclopoid copepods	2	0.8	0.12
10	Polychaetes	1	1.5	0.12
11	Isopods	2	0.5	0.08
12	Demersal eggs	1	0.8	0.06
13	Echinoids	1	0.4	0.03
14	Ostracods	1	0.1	<0.01
Also,	crustacean fragments	7	10.8	5.82
	Sand and foraminiferans	3	4.5	1.04
	Algal fragments	2	1.2	0.18
	Unidentified fragments	10	35.0	26.92

The widespread occurrence of this fish probably relates to the fact that no single item, or certain few items, especially predominate in its diet. This is true to an even greater degree in the ubiquitous *Thalassoma duperrey,* above, but is unlike most fishes on Kona reefs.

CONCLUSION.—*Halichoeres ornatissimus* is a diurnal predator that picks a wide variety of small benthic animals from the sea floor.

Stethojulis balteata **(Quoy and Gaimard) — *'omaka***

This wrasse is most numerous on the shallow reef flats and on some of the reefs richly overgrown with corals. During the day it swims close to rocks or coral, at which it periodically picks. At night it rests in reef crevices, or buried in the sand.

All five specimens (90: 76-102 mm) collected during daylight had a gut full of material, some of it fresh, as listed in Table 55. The major food items—small crustaceans shorter than about 4 mm—were mostly intact. Larger items, such as some of the gastropods, were crushed.

CONCLUSION.—*Stethojulis balteata* is a diurnal predator that mostly picks small crustaceans and gastropods off the sea floor.

Anampses cuvier **Quoy and Gaimard—*'opule***

Although this wrasse occupies all inshore reef habitats in Kona, it is most numerous where the sea floor consists of basalt boulders. During the day, solitary individuals swim close to the substratum, where they inspect the surface, and frequently pluck at the low growth of algae on the

TABLE 55.—Food of *Stethojulis balteata*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Harpacticoid copepods	5	19.4	19.40
2	Prosobranch gastropods	4	15.6	12.48
3	Gammaridean amphipods	3	8.6	5.16
4	Tanaids	3	5.0	3.00
5	Foraminiferans	2	2.4	0.96
6	Isopods	2	2.4	0.96
7	Polychaetes	1	4.0	0.80
8	Echinoids	1	1.0	0.20
9	Sipunculid introverts	1	0.6	0.12
10	Cyclopoid copepods	1	0.4	0.08
Also,	crustacean fragments	5	15.0	15.00
	Sand and debris	4	10.2	8.16
	Unidentified fragments	4	15.4	12.32

TABLE 56.—Food of *Anampses cuvier*.

Rank	Items	No fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	10	28.9	24.08
2	Mollusks	10	18.1	15.08
3	Polychaetes	3	4.3	1.08
4	Xanthid crabs	3	1.8	0.45
5	Fish eggs, demersal	1	5.0	0.42
6	Echinoids	2	1.9	0.32
7	Tanaids	3	0.3	0.08
8	Isopods	3	0.3	0.08
9	Didemnid tunicates	2	0.3	0.05
Also,	crustacean fragments	9	14.1	10.58
	Sand and foraminiferans	4	4.3	1.43
	Algal fragments	3	1.9	0.48
	Unidentified fragments	8	18.8	12.53

rocks. Much sand has accumulated here, and periodically they pause during their foraging to blow a small cloud of sand and debris from their mouths. At night this wrasse is out of sight, presumably resting in reef crevices.

All 12 specimens (169: 110-225 mm) speared during daylight had a gut full of material, much of it fresh, as listed in Table 56. The gammaridean amphipods, all shorter than 3 mm, were the major prey of even the largest individuals. Furthermore, the mollusks, which were the only other significant prey, were mostly prosobranch gastropods also shorter than 3 mm.

Undoubtedly, the small size and other characteristics of these prey are reflected in the feeding morphology of *A. cuvier* and its congeners, certain features of which set them apart from most other labrids in Kona. In dentition, the species of *Anampses*, with two flattened teeth projecting forward from the front of each jaw, are unlike those of any other genus of Hawaiian fishes (Gosline and Brock, 1960). Obviously this specialized dentition effectively captures gammarideans that inhabit the low stubble of algae overgrowing most basalt boulders. Compared with most other labrids, species of *Anampses* have the pharyngeal teeth reduced, which is expected considering the relatively small proportion of crushed items in the diet. The food items are mostly so small they need not be crushed upon ingestion. Gammarideans and certain other prey of similar size regularly pass intact through the pharynx of even those labrids with well-developed pharyngeal teeth (see accounts of other labrids in this report).

CONCLUSION.—*Anampses cuvier* is a diurnal predator that mostly plucks small benthic organisms, especially gammarideans, from rocky substrata.

Coris gaimard (Quoy and Gaimard)— *hinalea lolo*

This wrasse is most numerous where the reef is interspersed with small patches of sand. It forages in this sand during daylight, usually close to the base of rock or coral. Of all the wrasses treated in this report, this one is the most adept at excavating buried organisms. Moving its head sidewise, it effectively overturns small stones or digs in the

TABLE 57.—Food of *Coris gaimard*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Mollusks	9	72.2	72.20
2	Echinoids	3	9.8	3.27
3	Crabs	1	2.2	2.44
4	Didemnid tunicates	1	0.6	0.07
5	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		5	15.0	8.33

TABLE 58.—Food of *Macropharyngodon geoffroy*.

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	8	37.8	37.80
2	Foraminiferans	8	35.3	35.30
3	Harpacticoid copepods	2	0.4	0.10
4	Gammaridean amphipods	1	0.1	0.01
Also, crustacean fragments		2	0.6	0.15
	Sand and algae	5	8.4	5.25
	Unidentified fragments	6	17.4	13.05

sand, exposing hidden prey. It is not seen at night, when presumably it is buried in the sand, or secreted in reef crevices.

All nine specimens (117: 81-164 mm), speared during daylight, contained relatively fresh material, but items longer than a few millimeters were crushed so extensively that precise identifications were difficult. The gut contents are itemized in Table 57.

CONCLUSION.—*Coris gaimard* is a diurnal predator that mostly excavates mollusks and other prey that are buried in the sand.

Macropharyngodon geoffroy (Quoy and Gaimard)

This solitary little wrasse is widespread on Kona reefs, but is nowhere numerous. It swims close among coral and rocks during daylight, but is not seen after dark, when presumably it secretes itself in reef crevices, or under the sand.

All eight specimens (99: 74-120 mm) collected during the day had the gut full of the items listed in Table 58, almost all crushed.

The exceptionally large pharyngeal teeth of this wrasse obviously are adapted to a diet of heavily shelled organisms. The specimens examined, which had fed mostly on gastropods and foraminiferans, are undoubtedly representative. The foraminiferans were almost all *Marginospora vertebralis,* which is an abundant benthic form on shallow reefs in the Marshall Islands (Cushman, Todd, and Post, 1954).

CONCLUSION.—*Macropharyngodon geoffroy* is a diurnal predator that feeds mostly on benthic gastropods and foraminiferans.

Gomphosus varius Lacépède—bird wrasse, *hinalea 'i'iwi*

This wrasse is numerous on shallow surge-swept reefs, especially where the coral *Pocillopora meandrina* abounds. During daylight solitary individuals swim among the coral heads, probing with their elongated snouts among the coral branches. At night the species lies quietly in reef crevices.

All 12 specimens (142: 114-180 mm) collected during the day had their guts full of the items listed in Table 59. Most of this material was crushed. The xanthid crabs were mostly *Trapezia* sp. They and the alpheids are species that live among the branches of *P. meandrina.* Hiatt and Strasburg (1960) noted that this labrid's major prey in the Marshall Islands are xanthids and alpheids that live in the interstices of ramose corals. Randall (1955) similarly reported alpheid shrimps and also stomatopods in the diet of this species (as *G. tricolor)* in the Gilbert Islands.

Gomphosus varius takes relatively large motile prey, and with its large mouth does not pluck them from the substratum in the manner characteristic of the many other wrasses that prey on relatively tiny or sessile organisms. Rather, this wrasse vigorously wrests its prey from the reef crevices in which they are secreted.

TABLE 59.—Food of *Gomphosus varius*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	37.9	22.11
2	Alpheid shrimps	2	6.7	1.12
3	Pelecypods	1	4.2	0.35
4	Gastropods	2	2.1	0.35
Also, crustacean fragments		8	25.8	17.20
	Unidentified fragments	4	23.3	7.77

CONCLUSION.—*Gomphosus varius* is a diurnal predator that takes relatively large crustaceans from reef crevices.

General Remarks on Wrasses

Kona reefs, like tropical reefs the world over, are populated by a diverse array of wrasses, most of them with strong pharyngeal teeth adapted to crush hard-bodied prey. *Macropharyngodon geoffroy,* for example, preys on more heavily armored prey—in this case mollusks and foraminiferans. Others, like *Anampses cuvier,* have the pharyngeal teeth less developed and prey mostly on tiny crustaceans. Some of the wrasses, especially *Thalassoma duperrey,* are highly opportunistic, and these tend to be the most widespread and have the most varied diets.

It is well known that wrasses are active only during the day; at night they rest in reef crevices and under the sand (Longley and Hildebrand, 1941; Gosline and Brock, 1960; Hobson, 1965, 1968a, 1972; Starck and Davis, 1966; Collette and Talbot, 1972). They are among the first diurnal fishes on the reef to seek cover at day's end, and among the last to leave cover in the morning (Hobson, 1965, 1968a, 1972; Collette and Talbot, 1972).

Family Scaridae: parrotfishes

Scarus sordidus Forskål—*uhu*

This is one of the more numerous parrotfishes in Kona, especially over coral-rich reefs. During the day, it swims actively close to the substratum, often in groups. With its parrotlike beak, it scrapes away the fine filamentous algae that grows over the surface of dead coral, especially *Porites.* Although frequently it scrapes up to the edge of living coral, it stops there (Figure 34). During twilight, this species migrates in schools from one part of the reef to another, but the migratory pattern remains unclear (Hobson, 1972).

At night *S. sordidus* rests solitarily in reef crevices. Because some parrotfishes are known to secrete a mucous envelope around themselves at night (Winn, 1955), during a series of night observations over 3 mo I estimated the standard length of each resting parrotfish, and noted whether or not it was encased in mucus. During these observations, 20 individuals of this species were seen, estimated to be between 150 and 350 mm long. All eight that appeared to be shorter than 300 mm were in mucous envelopes, whereas all six without envelopes were judged to be longer than 300 mm. The other six, all estimated to exceed about 300 mm long, were in envelopes. Thus, all the smaller individuals, but only some of the larger ones, were in envelopes.

The guts of all seven *S. sordidus* (195: 150-213 mm) that were speared during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%). No evidence was found in these specimens of coral tissues or mucus (the latter is prominent in the gut contents of fishes known to feed on coral), even though Hiatt and Strasburg (1960) reported that coral polyps constituted the major food of this parrotfish in the Marshall Islands. These authors stated (p. 103): "Scraping living coral heads seems to be its predominant mode of feeding." This observation contrasts with mine in Kona, where *S. sordidus* avoids the living coral when feeding.

CONCLUSION.—*Scarus sordidus* is a diurnal herbivore that feeds mostly by scraping fine benthic algae that have overgrown the surface of dead coral.

Scarus taeniurus Valenciennes—*uhu*

My observations of their social interactions render it clear that the two forms Schultz (1969) distinguished in Hawaii as *S. taeniurus* and *S. forsteri* are conspecific and that his "*S. forsteri*" represents the large male of the species.

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night after night to caves in the same areas, but not necessarily to the same cave, as has been reported for some parrotfishes elsewhere (e.g. Winn and Bardach, 1960; Starck and Davis, 1966).

The guts of two males (340 and 410 mm) that were speared during midday were full of bits of algae mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus rubroviolaceus* is a diurnal herbivore that typically scrapes benthic algae from rock surfaces.

General Remarks on Parrotfishes

It is well known that parrotfishes are quiescent at night. They have been thus described in the tropical Atlantic (Winn, 1955; Winn and Bardach, 1959, 1960), eastern Pacific (Hobson, 1965; Rosenblatt and Hobson, 1969), Hawaii (Hobson, 1972), and elsewhere. Earlier (Hobson, 1965), I suggested that mucous envelopes in resting parrotfishes at night are characteristic of certain small individuals, or of individuals suffering injury or stress. The relation between small size and envelope secretion was also noted by Starck and Davis (1966) and by Casimir (1971). Winn and Bardach (1959) believed that the envelope is a defense against nocturnal predators, especially those that sense prey by olfaction or gustation, as do certain moray eels (Bardach, Winn, and Menzel, 1959). Because the threat from predators increases with decreasing size, obviously the smaller individuals are in greatest need for protection. Similarly, it is known that injured or distressed fishes are particularly attractive to predators (e.g. Hobson, 1968a), so envelope secretion by parrotfishes suffering these conditions is consistent with the idea that the envelopes provide protection. The survey of mucous envelopes in Kona shows a decreasing incidence with increasing size. Nevertheless, Winn and Bardach (1960), working with *Scarus vetula* at Bermuda, found that certain individuals in aquaria produced the envelope irregularly, and Smith and Tyler (1972) found that one individual of that species observed on a reef in the Virgin Islands formed an envelope on some nights, but not on others. Probably this variation within individuals occurs in other species too, but the question was not examined in Kona, where only certain males of *S. rubroviolaceus* were recognized as individuals, and these were never seen in envelopes.

There is controversy over the diet of parrotfishes. Hiatt and Strasburg (1960) reported a diet of living coral not only in *S. sordidus,* as noted above, but also in all other scarids they examined in the Marshall Islands. I found no evidence that any of the species in Kona, including *S. sordidus,* feed on living coral. Randall (1967) similarly concluded that parrotfishes in the West Indies do not feed on living coral; he noted the large amount of sand in the guts of parrotfishes, and suggested that this material, taken purposefully, aids in grinding plant tissue—the primary food —in the pharyngeal mill.

Although I classify all parrotfish species in Kona as herbivores, their large gut loads of calcareous powder, organic slurry, and sand seem too great a proportion of the total contents to have been taken only incidentally, or to be adaptive only because it aids in grinding up plant tissue. There is need to look closer at how parrotfishes utilize the material they ingest.

Family Blenniidae: combtooth blennies

The combtooth blennies are most numerous in tide pools and close to rocky shores, where frequently they are the dominant fishes. However, this report considers only those species that occur regularly in water deeper than 5 m.

Exallias brevis (Kner)—*pao'o kauila*

Because *E. brevis* is distinctively hued and habitually perches in exposed positions during the day (Figure 37), it is frequently noticed even though it is not especially numerous. It rarely leaves the sea floor and usually rests immobile except when scraping the surface of living coral with its comblike teeth. After dark, it is secreted in reef crevices and seen only occasionally.

Of the 10 specimens (94: 70-106 mm) examined, 2 that were taken from under partial cover at night (between 4 and 5 h after sunset) contained only well-digested fragments, whereas only 1 taken during the day was empty, and the other 7 were full of food, including fresh material. The major item in all seven (over 90% of the contents in each) was scleractinian corals—both skeletal and tissue fragments, along with much mucus. The remaining identifiable items in the diet were fine filamentous algae and diatoms.

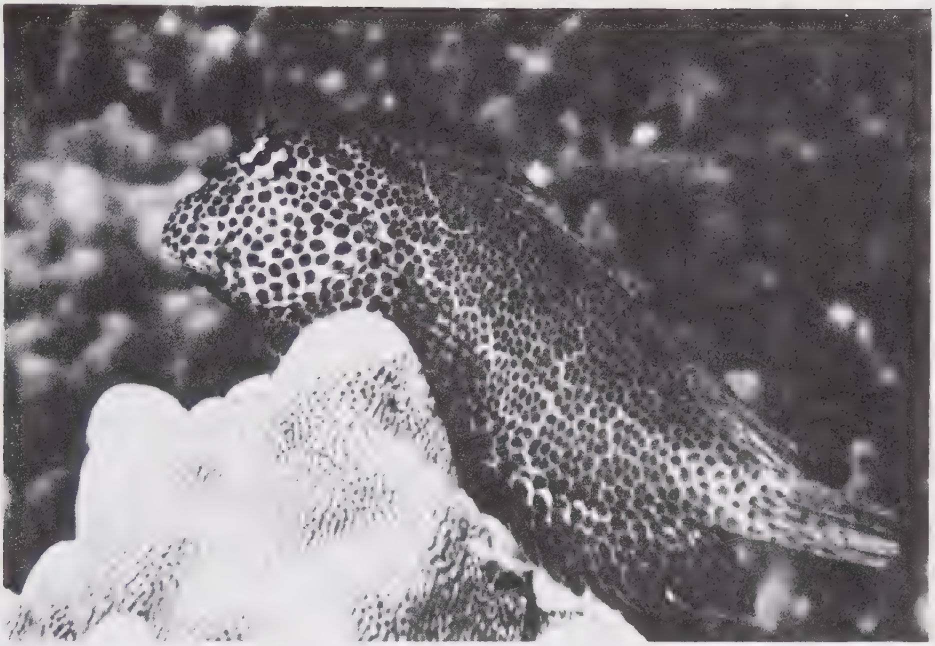

FIGURE 37.—*Exallias brevis,* a blenny, showing typical diurnal attitude.

In contrast to these food data, Hiatt and Strasburg (1960) found only filamentous algae and detritus in the single *E. brevis* (80 mm) that they examined in the Marshall Islands.

CONCLUSION.—*Exallias brevis* is a diurnal species that feeds largely on scleractinian corals, both tissue and mucus.

Cirripectus variolosus (Valenciennes)

During the day, this relatively small blenny moves about close to cover on the reef, remaining in contact with the substratum. Though numerous, it is not seen after dark, when presumably it is secreted in reef crevices.

The guts of both specimens (66 and 80 mm) collected during midday contained filamentous algae (about 40% of the diet volume) and what appeared to be detritus (50 to 60%). In addition, one contained a few scleractinian coral fragments (5%). Except for the coral fragments, the diet of these two individuals was the same as that of one specimen of this species examined by Hiatt and Strasburg (1960) in the Marshall Islands.

CONCLUSION.—*Cirripectus variolosus* is a diurnal species that feeds mostly on algae and detritus.

Plagiotremus goslinei (Strasburg)—sabre-toothed blenny

During the day, *P. goslinei* hovers a meter or so above the reef, from which position it attacks larger fishes that incidentally pass by, striking them unseen from below and behind, much as does *P. azalea* in the eastern Pacific (Hobson, 1968a, 1969). But whereas *P. azalea* usually aggregates when hovering above the reef, *P. goslinei* usually is solitary. No specimens of *P. goslinei* were collected, but presumably it feeds on the mucus and dermal tissue of its victim, as do other species of this genus, including *P. rhinorhynchus* (Wickler, 1960), *P. azalea* (Hobson, 1968a), and *P. townsendi* (Springer and Smith-Vaniz, 1972). These species are called sabre-toothed blennies because each carries in its lower jaw a pair of enormous fangs. Eibl-Eibesfeldt (1955) and Strasburg (1960) believed that these fangs are used in feeding, but Wickler (1960) concluded from work in aquaria that *P. rhinorhynchus* uses its fangs not to feed, but rather to defend its territory.

Plagiotremus goslinei hovers above the reef during only part of the day. Much of the time it occupies abandoned mollusk and worm tubes on the rocks, and these retreats also serve as resting places at night. In the eastern Pacific, *P. azalea* uses similar tubes in the same way (Hobson, 1968a, 1969).

CONCLUSION.—*Plagiotremus goslinei* is a diurnal predator that feeds on mucus and dermal tissue of larger fishes.

General Remarks on Combtooth Blennies

The combtooth blennies are generally regarded as diurnal. For example, Starck and Davis (1966) did not see members of the family, known to be present, during many night observations on Florida reefs, and Randall (1967) reported the group to be diurnal in the West Indies.

Although food habits remain unknown or uncertain for most combtooth blennies, reportedly many feed by scraping filamentous algae and detritus from rocks. These items predominated in the diet of all four blenniid species that Randall (1967) examined in the West Indies, and in all five studied by Hiatt and Strasburg (1960) in the Marshall Islands. In Kona, this mode of feeding occurs in *Cirripectus variolosus*, but *Exallias brevis* may be exceptional in feeding mostly on the tissue and mucus of scleractinian corals. The significance of coral mucus as food of *E. brevis* may relate to the significance of fish mucus as food for blennies of the genus *Plagiotremus*. Böhlke and Chaplin (1968) suggested that at least some combtooth blennies which scrape algae from rocks may gain most of their nourishment from small organisms living on or around the algae. Clearly, much about blenniid feeding remains unknown. Because these small fishes scrape their food from various substrata, their gut contents are difficult to analyze. One can easily see that species of *Plagiotremus* have a mode of feeding that differs from those of other blenniids, because their manner of taking food is uniquely spectacular. In comparison, differences distinguishing the feeding modes of other combtooth blennies are relatively subtle.

Family Acanthuridae: surgeonfishes

The surgeonfishes are the predominant fishes over most Hawaiian inshore reefs, but this report treats only the two species that feed on zooplankton in the water column. The habits of these two were only superficially touched on by Jones (1968), who provided a thorough treatment of the many species occurring in Kona that take their food directly from the substratum (see general remarks on surgeonfishes, below).

Acanthurus thompsoni (Fowler)

Acanthurus thompsoni (Figure 38) swims in stationary aggregations in the water column above the reef in several locations along the outer drop-off, 20 to 30 m deep. Often mixed with this surgeonfish in these groups are several other species, especially *Chromis verater, C. ovalis,* and *Naso hexacanthus*. At nightfall, *A. thompsoni* descends to the reef below where, inactive but alert, it remains under cover until morning.

Fourteen individuals (141: 128-185 mm) were speared at different times of day and night. All six that were taken from crevices during the hour before daybreak had empty stomachs, whereas, all seven collected from aggregations in the water column at various times during afternoons had full stomachs, including fresh material. Finally, one solitary individual speared during midafternoon close among the coral in about 6 m of water, approximately 200 m from the nearest feeding aggregation, had its stomach empty. The seven individuals with material in their stomachs contained the items listed in Table 60.

The data show a strong trend in the diet toward relatively large, semitransparent, and often gelatinous prey. Some planktivorous fishes from other families feed heavily on one or another of these prey, as does the pomacentrid *Chromis verater,* which feeds heavily on larvaceans (see species account, above). But in none of these others is the diet similarly dominated by an array of such prey. However, the sparse information on the food habits of *A. thompsoni* given by other authors does not show this trend. Gosline and Brock (1960) reported only mollusk eggs and copepods, whereas Jones (1968) noted copepods, crab zoea, crab megalops, and mysids. But these reports did not indicate how many specimens were examined, nor the relative proportion of each type of prey in the diet. Most important, they did not indicate how much of the gut contents remained unidentified. The major food items that I found in *A. thompsoni* are types quickly rendered unidentifiable by digestion, and thus easily missed if the sample is not fresh.

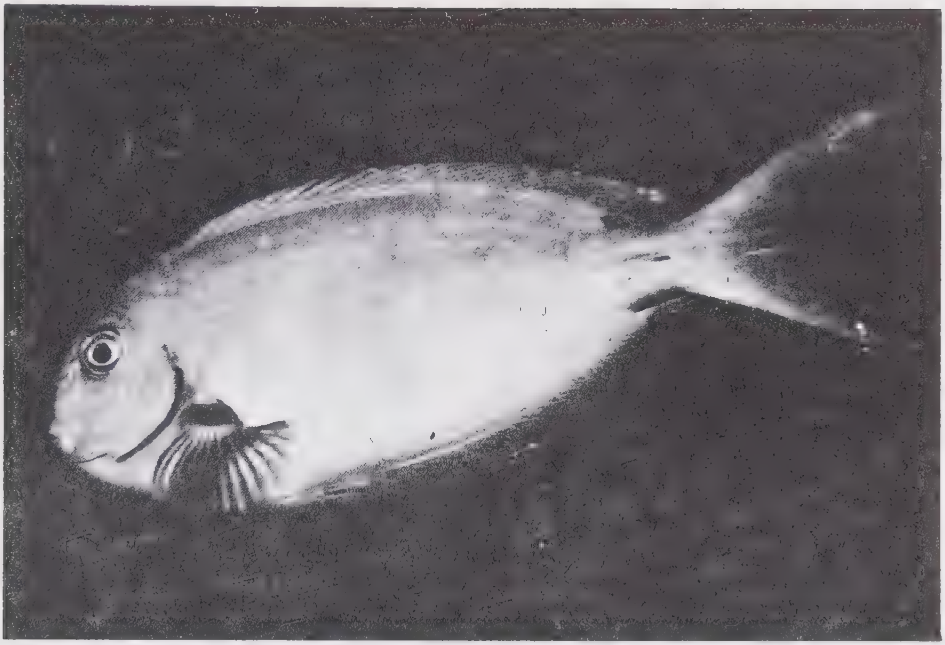

FIGURE 38.—*Acanthurus thompsoni*, a zooplanktivorous surgeonfish. In comparison with its bottom-feeding congeners, this species carries its more upturned mouth higher on its head, its body is more fusiform, and its tail is more deeply lunate. These morphological tendencies occur in many unrelated zooplanktivorous fishes.

CONCLUSION.—*Acanthurus thompsoni* is a diurnal planktivore that feeds mostly on semitransparent, often gelatinous, organisms—especially chaetognaths, salps, siphonophores, and larvaceans.

Naso hexacanthus (Bleeker)—*kala*

During daylight, this relatively large surgeonfish swims above the outer drop-off in schools that periodically range farther offshore to yet unknown distances. Brock and Chamberlain (1968) found this species at depths below 120 m when diving in the research submarine *Asherah*, but it is not known whether these fish had migrated from shallower water or are of deepwater populations, although the latter possibility seems the more probable. Generally, individuals in less than 10 m of water over inshore reefs during the day are relatively small, and swim in groups of

TABLE 60.—Food of *Acanthurus thompsoni*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Chaetognaths	6	37.1	31.80
2	Salps	7	18.6	18.60
3	Siphonophores	4	10.0	5.71
4	Larvaceans	5	7.4	5.29
5	Calanoid copepods	4	8.6	4.91
6	Gelatinous egg masses	2	1.7	0.49
7	Gelatinous clumps of blue-green algae	2	1.6	0.46
8	Fish eggs, planktonic	2	1.3	0.37
9	Hyperiid amphipods	3	0.7	0.30
10	Polychaetes	2	0.9	0.26
11	Decapod shrimps	1	0.3	0.04
12	Harpacticoid copepods	1	0.1	0.01
Also, unidentified fragments		4	11.7	6.69

only a few individuals, often close to the substratum. Most representatives seen inshore are not feeding, but rather move uniformly together closely spaced in schools. When they do feed, the schools are abandoned for aggregations in which loosely spaced individuals act independently.

During evening twilight many individuals move in from deeper water over the shallower parts of the reef. Larger representatives are in the shallows only after dark. On dark nights, the species is scattered close among rocks and corals, relatively inactive, but alert. However, on moonlit nights some swim above the reef in small groups.

Sixteen individuals (261: 202-392 mm) were speared at various times of night and day. Because larger individuals are less accessible, especially during the day, the sample is biased toward smaller members of the species. All four solitary individuals taken close among rocks or coral at night (later than 4 h after sunset and before daybreak) had empty stomachs, whereas only one of nine others taken from schools above the reef at various times of day had material in its stomach, and this one came from a school that had just appeared over the reef from offshore during midafternoon. Finally, all three that had been observed feeding when speared above inshore reefs (on three afternoons over 2 mo) had full stomachs. Items in the four individuals whose stomachs contained food are listed in Table 61.

Like *Acanthurus thompsoni,* this acanthurid feeds mostly on semitransparent, often gelatinous, prey. Of the four that contained food, the three taken from inshore feeding aggregations were relatively small fish (233-238 mm) whose major food was planktonic fish eggs. Perhaps significantly, there were no fish eggs in the fourth specimen, which had just appeared over the reef from offshore. This individual was larger than the others, about 300 mm long, but was collected within 30 min of one of them. The major item in its stomach was filamentous red algae, which did not occur in the smaller three. Only chaetognaths and larvaceans occurred in the stomachs of all four specimens. These limited data suggest there may be distinctive differences in diet and feeding grounds over the size range of individuals sampled.

The high incidence of empty stomachs among individuals over the inshore reefs during the day, as well as at night, suggests that many may feed offshore, and be relatively inactive, or at least not feeding, when they are inshore.

Jones (1968) included *N. hexacanthus* with *A. thompsoni* when reporting the diet of copepods, crab zoea, crab megalops, and mysids noted above. My comments concerning the reported diet of *A. thompsoni* (see above) apply equally here.

CONCLUSION.—*Naso hexacanthus* is a diurnal planktivore that takes mostly semitransparent, often gelatinous, prey—especially chaetognaths, larvaceans, and fish eggs. Limited data suggest that drifting pieces of filamentous algae may also be important.

General Remarks on Surgeonfishes

Surgeonfishes are widespread on tropical reefs, and usually are described in a general way as herbivores (e.g. in the Bahamas by Böhlke and Chaplin, 1968; and in the West Indies by Randall, 1967). Jones (1968) grouped the many Hawaiian surgeonfishes according to their habitats and methods of foraging. In categorizing the bottom-foraging species, not studied by me, he defined three types of habitats, and listed the surgeonfishes characteristic of each: 1) The turbulent

TABLE 61.—Food of *Naso hexacanthus.*

Rank	Items	No. fish with this item ($n = 4$)	Mean percent of diet volume	Ranking index
1	Chaetognaths	4	21.3	21.30
2	Fish eggs, planktonic	3	25.0	18.75
3	Larvaceans	4	16.3	16.30
4	Filamentous red algae	1	18.4	4.60
5	Decapod shrimps	3	2.3	1.73
6	Calanoid copepods	2	2.3	1.15
7	Siphonophores	2	2.0	1.00
8	Polychaetes	1	1.3	0.33
9	Hyperiid amphipods	1	0.5	0.13
10	Mollusk veligers	1	0.3	0.08
11	Gammaridean amphipods	1	0.3	0.08
Also, unidentified fragments		2	10.0	5.00

waters of the surge zone are frequented by four species of *Acanthurus* (*achilles, glaucopareius, guttatus,* and *leucopareius*). 2) The sand patches on deeper, more tranquil reefs are home to four species of *Acanthurus* (*dussumieri, mata, olivaceus,* and *xanthopterus*). 3) Finally, basalt and coral substrata on reefs below the surge zone (to a depth of about 90 m) are inhabited by three species of *Acanthurus* (*nigrofuscus, nigroris,* and *sandvicensis*); two species of *Ctenochaetus* (*hawaiiensis* and *strigosus*); two species of *Zebrasoma* (*flavescens* and *veliferum*; the adults of the latter often occur in the surge zone); and three species of *Naso* (*brevirostris, lituratus,* and *unicornis*).

In erecting categories according to foraging types, Jones (1968) classified the bottom feeders either as browsers or grazers. The browsers are described as "strictly herbivores that bite and tear off bits of multicellular benthic algae, generally without ingesting any of the inorganic substratum." Browsing surgeonfishes include those characteristic of the surge zone and those characteristic of subsurge reefs, except for the two *Ctenochaetus*. The browsing species of *Acanthurus* and *Zebrasoma* feed chiefly on fine filamentous algae, whereas the browsing species of *Naso* tend to feed on the leafy and fleshy forms.

Surgeonfishes classified by Jones (1968) as grazers are described as "Fishes that purposely pick up large quantities of the substratum while feeding. . . irrespective of whether the material is rasped away from rocks, or picked up as loose sand." This category includes the surgeonfishes characteristic of the sand patches, all of which are species of *Acanthurus,* and the two reef-dwelling species of *Ctenochaetus*. The sand-patch *Acanthurus* species pick up mouthfuls of sand, whereas the reef-dwelling *Ctenochaetus* species ingest sediment that has accumulated over rocks and dead coral. In examining these sediment-packed guts, Jones found material from the two groups distinguishable by particle size—being coarse and grainy in the sand-patch *Acanthurus,* fine and silty in the reef *Ctenochaetus*. He concluded that the major food of both groups are diatoms and detritus that have accumulated around the particles in the surface layers of the sediment.

Surgeonfishes are widely recognized to be active by day and relatively inactive at night (e.g. in the Gulf of California by Hobson, 1965; and in the Florida Keys by Starck and Davis, 1966). Although quiescent, these nocturnally resting acanthurids are most often described as alert; however, Collette and Talbot (1972) reported that *Acanthurus coeruleus* sleeps while sheltered among coral at night in the Virgin Islands. In the Gulf of California, *Prionurus punctatus* aggregates above the reef on bright moonlit nights (Hobson, 1965), as does *Naso hexacanthus* in Kona.

Family Zanclidae: moorish idol

Zanclus canescens (Linnaeus)—
moorish idol, *kihikihi*

The moorish idol (Figure 39a) is closely related to the surgeonfishes, and some ichthyologists (e.g. Greenwood et al., 1966) consider it to be a member of that family. It lacks the caudal spine common to all surgeonfishes, however, and most classifications assign it to the monotypic family Zanclidae.

This fish is numerous in all Kona inshore habitats, where it swims over the reef during the day, usually in groups of four to six individuals. When feeding, it regularly probes the narrow cracks and crevices of the reef with its elongated snout. At night it is relatively inactive, but alert, close among rocks or coral, and at this time its coloration differs strikingly from that displayed in daylight (compare Figure 39a and b).

Of 21 specimens (108: 74-137 mm) speared at various times of day and night, all 9 that were collected at night (later than 4 h after sunset and before sunrise) had empty stomachs, whereas all 12 that were taken during the day (between midmorning and late afternoon) had full stomachs that included fresh material. Items in the specimens containing identifiable material are listed in Table 62.

The sponges, which greatly predominate in the diet, were all small species that presumably live in narrow reef crevices. This fish appears to be specialized in this diet, although Randall (1955) reported only algae in two specimens from the Gilbert Islands.

CONCLUSION.—*Zanclus canescens* is a diurnal species that feeds mostly on small sponges.

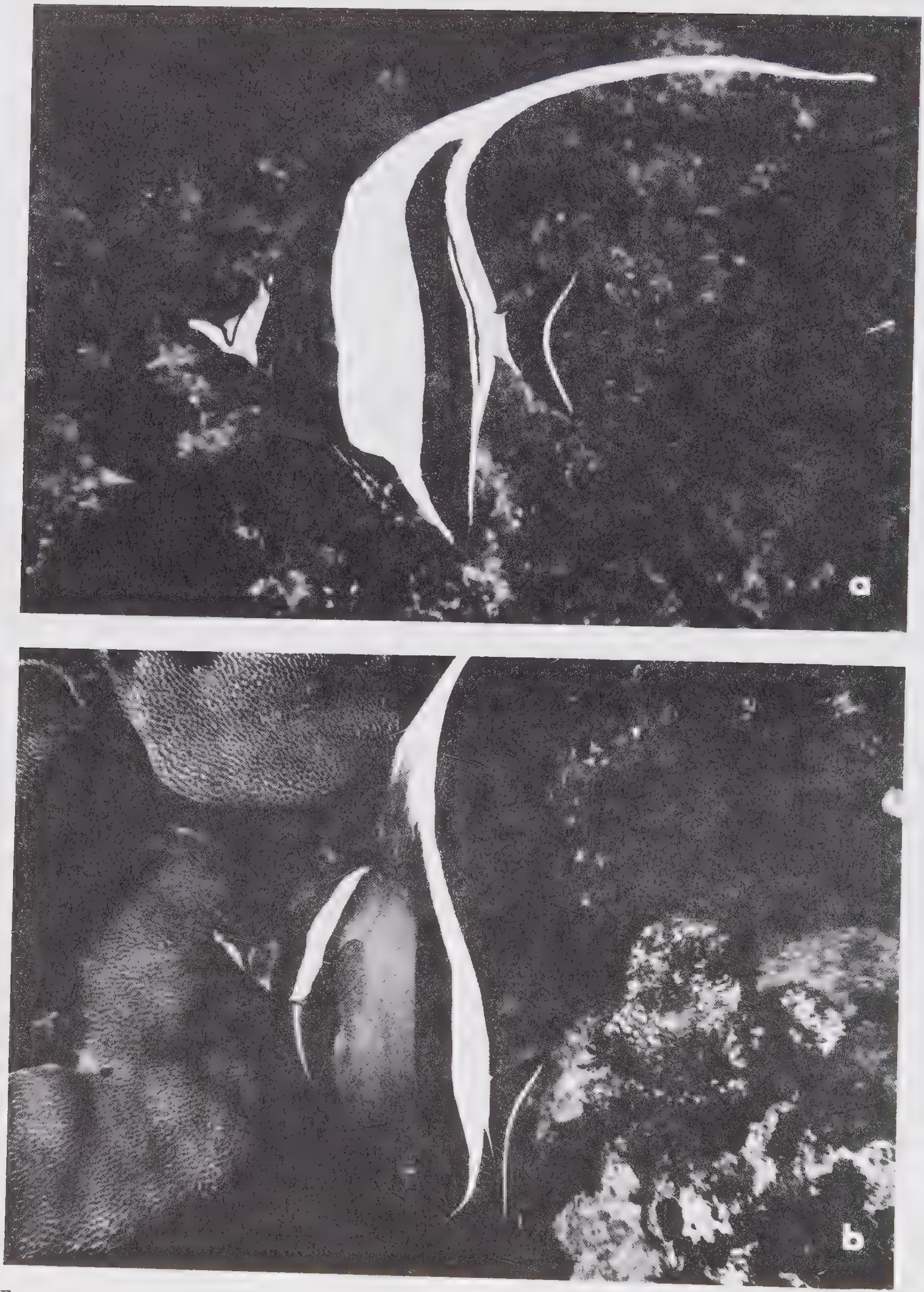

FIGURE 39.—*Zanclus canescens*, the moorish idol: a, showing diurnal coloration while swimming over the reef during the day; b, showing nocturnal coloration while close to the reef at night.

TABLE 62.—Food of *Zanclus canescens*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Sponges	12	84.5	84.50
2	Coralline algae	12	5.7	5.70
3	Other algae	12	5.6	5.60
4	Bryozoans	8	1.1	0.73
5	Pelecypod mollusks	8	0.9	0.60
6	Gammaridean amphipods	6	0.5	0.25
7	Polychaetes	4	0.6	0.20
8	Foraminiferans	3	0.3	0.08
9	Hydroids	2	0.2	0.03
10	Barnacle cirri	2	0.2	0.03
11	Didemnid tunicates	1	0.2	0.02
12	Tanaids	1	0.1	<0.01
13	Decapod shrimps	1	0.1	<0.01

ORDER PLEURONECTIFORMES

Family Bothidae: left-hand flounders

Bothus mancus (Broussonet)—*paki'i*

This flatfish is most numerous lying immobile where rocks are interspersed with small patches of sand. It changes its coloration to match closely that of whatever substratum it happens to lie on, rocks or sand. When on sand, it is frequently buried except for its eyes. No change was noted in the overt behavior of this fish between day and night.

Eight specimens (223: 137-277 mm) were speared at various times of the day. Both individuals collected within an hour after sunrise were empty, whereas of six taken during afternoons, two were empty and four contained well-digested fish remains that appeared to have been in the stomachs at least several hours when collected.

Hiatt and Strasburg (1960) reported this flounder on both rocks and sand in the Marshall Islands and noted a diet comprised primarily of fishes that live in sandy areas adjacent to coral. Most prey species listed by them are fishes (balistids, labrids, pomacentrids, and blennies) that probably are active in exposed positions only during daylight. They believed that *B. mancus* responds only to moving prey; if so, at least most of its prey, which rests at night, would not be available after dark. The prey listed by Hiatt and Strasburg also included two species of apogonids, members of what seems to be a universally nocturnal group; however, during daylight these particular apogonid species congregate in exposed positions close among the coral, where they would seem available to diurnal predators.

CONCLUSION.—*Bothus mancus* preys on small fishes during the day. Its nocturnal habits remain uncertain.

General Remarks on Left-hand Flounders

Bothids are the most numerous flatfishes on tropical reefs. In the West Indies, Randall (1967) found fishes the major prey of *Bothus lunulatus* and *B. ocellatus*, both of which occur on sand patches around coral reefs, often largely buried. In the Florida Keys, Starck and Davis (1966) found *B. ocellatus* in sandy areas of all reef zones, and although they did not examine its food habits, they inferred from its behavior that it preys after dark on the various small nocturnal invertebrates active on the sand at night.

ORDER TETRAODONTIFORMES

Family Balistidae: triggerfishes

Melichthys niger (Bloch)—*humuhumu 'ele'ele*

During the day, *M. niger* typically hovers in loosely spaced aggregations several meters above the reef. Each individual independently picks material drifting in the mid-waters. It is a wary animal that dives to holes in the reef when alarmed. It enters these same holes at nightfall and rests there on its side until morning.

All seven individuals (165: 122-195 mm) speared from among those active above the reef during the day were full of food, as listed in Table 63. The major food items are fragments of fleshy algae—filamentous and foliaceous—probably most of which are drifting in the mid-waters when taken. This triggerfish feeds at least occasionally on the sea floor, as indicated by the relatively high

TABLE 63.—Food of *Melichthys niger*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Fleshy algae	7	52.3	52.30
2	Coralline algae	7	18.7	18.70
3	Calanoid copepods	5	2.7	1.93
4	Caridean shrimps	4	1.1	0.63
5	Harpacticoid copepods	4	0.6	0.34
6	Scleractinian coral	1	2.1	0.30
7	Insects	2	0.4	0.11
8	Foraminiferans	2	0.3	0.09
9	Heteropods	2	0.3	0.09
10	Cyclopoid copepods	1	0.6	0.09
11	Crab megalops	1	0.4	0.06
12	Mollusk veligers	1	0.1	0.01
13	Naticid gastropods	1	0.1	0.01
14	Ostracods	1	0.1	0.01
15	Gammaridean amphipods	1	0.1	0.01
16	Fish eggs, planktonic	1	0.1	0.01
Also, sand		1	2.9	0.41
	Unidentified fragments	6	17.1	14.66

proportion of coralline algae in its diet and also by the stony coral, bitten off in chunks, in one individual; nevertheless, most of its food is planktonic. Certainly the relatively minor status of the many zooplankters in the above list far understates their relative significance to this fish. The ranking is biased toward the more bulky items; thus, one algal fragment, in terms of volume, may be equivalent to a hundred or more copepods. And yet the effort expended in taking the algal fragment may have been no greater than that expended in taking a single copepod. A given volume of copepods (and many other zooplankters) probably is far more nutritious than the same volume of algae.

In the West Indies, this circumtropical triggerfish similarly feeds on algae and zooplankton in the mid-waters, taking the algae from the benthos, or as drifting fragments (Randall, 1967).

CONCLUSION.—*Melichthys niger* is a diurnal omnivore that feeds mostly on drifting algal fragments and zooplankton, along with some benthic vegetation.

Xanthichthys ringens (Linnaeus)

This triggerfish (Figure 40) is one of the most numerous fishes at depths below 25 m along the outer drop-off. Like so many fishes that concentrate in this location, it aggregates in the water column and picks plankton, an activity that is limited to daylight; at nightfall, it shelters in reef crevices, where it rests on its side until morning.

Of the 11 specimens (125: 98-145 mm) speared during day and night, 2 that were collected from reef crevices during the last hour before daybreak were empty, whereas all 9 that were taken from mid-water aggregations at various times during the day were full of food, as listed in Table 64.

I found no evidence that this triggerfish takes food from the sea floor. Like *Melichthys niger*, *X. ringens* is circumtropical (Böhlke and Chaplin, 1968); perhaps the planktivorous habits of these two triggerfishes permit survival over long periods in the open sea where their bottom-feeding relatives would perish. Gosline and Brock (1960), whose data were mostly from relatively shallow water, reported *X. ringens* uncommon in Hawaii. The large numbers of this species occurring along the outer drop-off in Kona, however, indicates a habitat in Hawaii similar to that in the West Indies, where it rarely occurs in less than 35 m of water, but is one of the most numerous fishes below that depth (Randall, 1968).

CONCLUSION.—*Xanthichthys ringens* is a diurnal planktivore that feeds mostly on calanoid copepods.

Rhinecanthus rectangulus (Bloch and Schneider)—*humuhumu nukunuku a pua'a*

This triggerfish is most common on shallow, surge-swept, basalt reefs. It is a solitary fish that swims close to the reef top during the day, picking at organisms on the bottom. A wary animal, it quickly takes refuge in the reef when threatened.

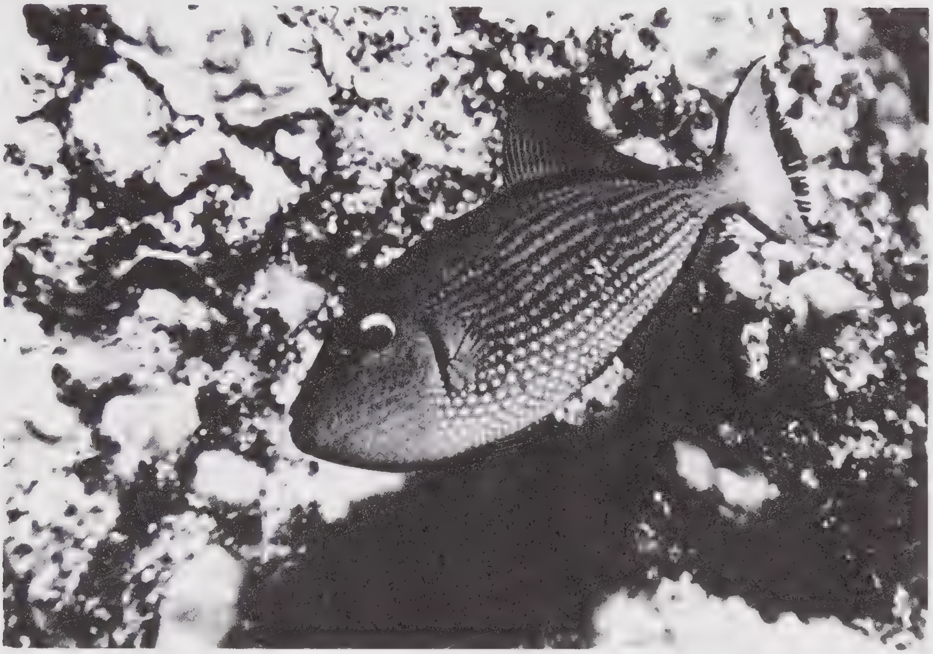

FIGURE 40.—*Xanthichthys ringens,* a zooplanktivorous triggerfish. In comparison with bottom-feeding triggerfishes, this species has a more upturned mouth that is higher on its head, and its body is more fusiform. Both features are widespread among zooplanktivorous fishes.

Its shelters, like those of *Melichthys niger,* above, are small enough so that the fish can wedge itself in by locking its large dorsal spine erect. Each individual fish seems to resort to a specific hole that serves as a refuge by day, and also as a resting place at night when the species is inactive.

All nine individuals (142: 114-170 mm) speared at various times of the day from among those active close to the reef were full of food, as listed in Table 65. Food items were mostly small organisms between 1 and 6 mm in their greatest dimension, taken intact; the few exceptions are fragments of about this size from larger organisms.

Hiatt and Strasburg (1960) found this species numerous on shallow reefs in the Marshall Islands and reported a crustacean and algal diet similar to that of the species in Kona.

TABLE 64.—Food of *Xanthichthys ringens.*

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	9	43.9	43.90
2	Mollusk veligers	6	0.8	0.53
3	Fish eggs, planktonic	2	1.4	0.31
4	Chaetognaths	2	1.3	0.29
5	Siphonophores	2	1.2	0.27
6	Pteropods	2	1.2	0.27
7	Ostracods	4	0.6	0.27
8	Cyclopoid copepods	1	0.8	0.09
9	Heteropods	2	0.3	0.07
10	Hyperiid amphipods	2	0.2	0.04
11	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		4	4.6	2.04
	Unidentified fragments	9	43.5	43.50

TABLE 65.—Food of *Rhinecanthus rectangulus.*

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	9	19.4	19.40
2	Didemnid tunicates	9	8.6	8.60
3	Filamentous algae	6	7.8	5.20
4	Xanthid crabs	4	6.7	2.98
5	Polychaetes	4	6.3	2.80
6	Decapod shrimps	5	4.2	2.33
7	Tanaids	4	2.9	1.29
8	Coralline algae	4	2.6	1.16
9	Prosobranch gastropods	4	2.4	1.07
10	Echinoids	3	2.9	0.97
11	Isopods	3	2.6	0.87
12	Bryozoans	2	0.7	0.16
13	Caprellid amphipods	1	0.6	0.07
14	Pelecypods	1	0.3	0.03
15	Crab megalops	1	0.2	0.02
Also, crustacean fragments		4	6.2	2.76
	Unidentified fragments	7	25.6	19.91

TABLE 66.—Food of *Sufflamen bursa.*

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Echinoids	9	9.1	9.10
2	Gammaridean amphipods	7	8.3	6.46
3	Polychaetes	8	4.6	4.09
4	Prosobranch gastropods	9	3.8	3.80
5	Brachyurans	5	4.8	2.67
6	Sponges	8	2.6	2.31
7	Tanaids	6	2.8	1.87
8	Opisthobranchs	6	2.3	1.53
9	Cyclopoid copepods	9	1.2	1.20
10	Isopods	7	1.3	1.01
11	Ostreid pelecypods	7	1.0	0.78
12	Caridean shrimps	3	0.8	0.27
13	Foraminiferans	4	0.4	0.18
14	Ostracods	4	0.4	0.18
15	Crab megalops	2	0.3	0.07
16	Bryozoans	1	0.1	0.01
17	Sipunculid introverts	1	0.1	0.01
18	Harpacticoid copepods	1	0.1	0.01
19	Barnacle cirri	1	0.1	0.01
20	Mites	1	0.1	0.01
Also, crustacean fragments		5	3.8	2.11
	Algal fragments	5	1.2	0.67
	Unidentified fragments	9	50.8	50.80

CONCLUSION.—*Rhinecanthus rectangulus* is a diurnal omnivore, feeding mostly on gammaridean amphipods and other small organisms.

Sufflamen bursa (Bloch and Schneider)— *humuhumu umauma lei*

This is the most numerous and widespread triggerfish on Kona reefs. A solitary species, active by day close to rocks and coral, it picks at organisms on the sea floor. It is less inclined to seek cover in reef crevices than are *Melichthys niger* and *Rhinecanthus rectangulus,* above, but nevertheless is a wary animal that shys away from humans. At night it is inactive, resting on its side under cover on the reef until morning.

Thirteen individuals (140: 109-164 mm) were speared at various times of day and night. The four that were collected in darkness as they rested in reef crevices during the last 2 h before daybreak were empty, whereas the nine that were collected at various times during the day as they swam over the reef were full of food, as listed in Table 66. As was true of the food of *R. rectangulus,* these food items, including the echinoids, are mostly small animals between 1 and 6 mm in their greatest dimension, taken intact; the exceptions are fragments of about this size from larger organisms. Unlike the omnivorous *R. rectangulus,* however, *S. bursa* seems to be strictly carnivorous (the few algal fragments among its gut contents probably were taken incidentally along with prey). No single item greatly predominates in its diet, a circumstance that may relate to its widespread occurrence in a variety of habitats.

CONCLUSION.—*Sufflamen bursa* is a diurnal predator that feeds on a variety of benthic animals.

General Remarks on Triggerfishes

The balistids are known for their powerful jaws and sharp cutting teeth, which enable them to prey on a variety of armored invertebrates denied as food to most other fishes (Randall, 1967). Most triggerfishes seem to make full use of this equipment: in the Virgin Islands *Balistes vetula* preys on the large echinoid *Diadema* (often attacking this sea urchin from its oral surface, where the spines are shortest) and on relatively large queen conchs, *Strombus,* which it crushes upon ingestion (Randall, 1967). Similarly, in the Marshall Islands several triggerfishes use their powerful feeding apparatus to crush mollusks and hard-shelled crustaceans, as well as to break off the tips of cespitose corals (Hiatt and Strasburg, 1960). *Rhinecanthus rectangulus* and *Sufflamen bursa* in Kona may be exceptional among bottom-foraging balistids in that they feed so heavily on small organisms, ingested intact. On the other hand, it may be that the high proportion of unidentified fragments in the guts of both species are the crushed remains of larger organisms not properly ranked among the data. Nevertheless, the capacity to feed on tiny organisms is probably well established among the balistids, as demonstrated by the exclusively zooplanktivorous habits of *Xanthichthys ringens.*

Triggerfishes are well known to be active by day and to rest under cover at night, usually lying on their sides. Diurnal habits were reported in balistids of the Gulf of California (Hobson, 1965, 1968a) and the West Indies (Randall, 1967). Collette and Talbot (1972) described *Balistes vetula* sleeping at night in exposed positions on reefs in the Virgin Islands, and Earle (1972) reported that in the Virgin Islands *B. vetula* frequently returns nightly to the same hole in the reef. There is at least some activity among triggerfishes on moonlit nights, however, as for example in *B. polylepis* in the Gulf of California (Hobson, 1965), but it is unknown whether this activity involves feeding.

Family Monacanthidae: filefishes

Cantherines dumerili (Hollard)—*'o'ili*

During daylight, this filefish swims several meters above coral-rich reefs, usually in loosely associated pairs that move, often on their sides, back and forth in restricted, well-defined areas. Because it swims in the water column and because it is relatively large, this filefish is a conspicuous component of the fauna, even though relatively few occur on the reef. Despite the time it spends in mid-water, *C. dumerili* was observed feeding only on the sea floor, where it bites off the tips of coral branches. During evening twilight it settles into holes in the reef, where it remains inactive until morning.

All eight individuals (200: 171-240 mm) speared from among those hovering above the reef during midday were full of food. Scleractinian corals were the major food items, occurring in seven of the eight specimens (mean percent of diet volume: 80; ranking index: 70), always as chunks of *Pocillopora* and *Porites,* about 4 mm in diameter. Other food items were: echinoids, all tips of the clublike spines of *Heterocentrotus mammillatus*, in two (mean percent of diet volume: 7.4; ranking index: 1.85), a variety of bryozoans, both encrusting and arborescent, that were almost the total contents of one (mean percent of diet volume: 12.5; ranking index volume: 1.56), and pelecypods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

Hiatt and Strasburg (1960) found that of the two specimens of this species (reported as *Amanses carolae)* that they examined in the Marshall Islands, one had fed on scleractinian corals exclusively, whereas the other had mixed a coral diet with sponges and algae. Apparently this species does not feed during the considerable time that it spends in the water column, as its diet seems to comprise only benthic organisms.

CONCLUSION.—*Cantherines dumerili* is a diurnal predator that feeds mainly on scleractinian corals.

Cantherines sandwichiensis (Quoy and Gaimard)—*'o'ili lepa*

This, the most numerous filefish in Kona, especially on basalt reefs in less than 10 m of water, is a solitary fish that swims close over the reef during

TABLE 67.—Food of *Cantherines sandwichiensis*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Filamentous algae	7	35.7	35.70
2	Coralline algae	7	32.1	32.10
3	Didemnid tunicates	7	6.1	6.10
4	Gammaridean amphipods	6	4.0	3.43
5	Scleractinian corals	2	5.0	1.43
6	Sponges	2	2.2	0.63
7	Diatoms	3	1.1	0.47
8	Bryozoans	2	1.0	0.29
9	Hydroids	2	0.4	0.11
10	Polychaetes	1	1.4	0.20
11	Ostreid pelecypods	2	0.6	0.17
12	Caprellid amphipods	2	0.6	0.17
13	Gastropod eggs	1	0.3	0.04
14	Prosobranch gastropods	1	0.3	0.04
15	Tanaids	1	0.1	0.01
16	Ophiuroids	1	0.1	0.01
Also, unidentified fragments		5	8.3	5.93
	Sand	1	0.7	0.10

TABLE 68.—Food of *Pervagor spilosoma*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	5	35.8	29.83
2	Filamentous algae	4	19.3	12.87
3	Coralline algae	6	7.7	7.70
4	Sponges	1	3.3	0.55
5	Polychaetes	2	1.5	0.50
6	Echinoids	3	0.8	0.40
7	Gammaridean amphipods	3	0.7	0.35
8	Tanaids	2	0.5	0.16
9	Diatoms	2	0.3	0.10
10	Fish eggs	1	0.5	0.08
11	Hydroids	2	0.3	0.10
12	Opisthobranch gastropods	1	0.2	0.03
13	Ostracods	1	0.2	0.03
14	Cyclopoid copepods	1	0.2	0.03
15	Crab megalops	1	0.2	0.03
16	Ophiuroids	1	0.2	0.03
Also, unidentified fragments		5	28.1	23.41
	Sand	1	0.2	0.03

the day, picking at objects on the bottom. During evening twilight, it moves from sight and is not visible at night when presumably it rests in reef crevices.

All seven individuals (116: 84-132 mm) speared from among those active close to the reef during the day were full of food, much of it fresh, as listed in Table 67.

CONCLUSION.—*Cantherines sandwichiensis* is a diurnal omnivore that feeds on a wide variety of benthic algae and invertebrates.

Pervagor spilosoma (Lay and Bennett)—*'o'ili 'uwi'uwi*

This, the most colorful filefish in Kona, as well as the smallest of the three considered there, is most numerous on coral-rich reefs. It is a solitary fish, active close among the corals in daylight, but not seen after dark when presumably it rests in reef crevices.

Of the seven specimens (85: 64-120 mm) collected, one that was speared close to coral just before sunrise (the first individual of the species to appear that morning) had an empty gut, whereas all six that were speared from among those active on the reef between midmorning and midafternoon were full of food, as listed in Table 68.

As is true of *Cantherines dumerili*, above, the major food of this filefish is scleractinian coral; however, whereas *C. dumerili* bites off relatively large chunks of coral, each containing many polyps, *P. spilosoma* seems to pluck at only one polyp at a time, as do certain chaetodontids. Nevertheless, judging from its gut load of skeletal fragments, *P. spilosoma* does not neatly snip off the polyps so much as coarsely gouge them from their thecae.

CONCLUSION.—*Pervagor spilosoma* is a diurnal omnivore that feeds mainly on scleractinian corals, to a lesser extent on algae and other benthic invertebrates.

General Remarks on Filefishes

In summarizing their treatment of monacanthids in the Marshall Islands, Hiatt and Strasburg (1960:105) stated: "There is no question that filefishes derive the bulk of their nutriment from living corals." All of the *Oxymonocanthus longirostris* (a widespread Indo-Pacific species that does not occur in Hawaii) examined by them contained only coral polyps, with no skeletal material. Their account indicates that this species, which has a very long, narrow snout, with teeth protruding from its mouth as long, cupshaped incisors, may be among the most highly specialized of coral-feeding filefishes. On the other hand, Randall (1967) found corals to be insignificant as food for West Indian filefishes; of the six species he examined, corals were in the diet of only one, and only as a minor component. According to Randall, the West Indian filefishes take a diverse array of benthic organisms: Algae and sea grasses are major items, along with a variety of benthic invertebrates. Thus, *Cantherines sandwichiensis* in Kona has a diet much like the West Indian species described by Randall, whereas *C. dumerili* takes largely corals in Kona, just as Hiatt and Strasburg reported it and other filefishes doing in the Marshall Islands. Clearly, many filefishes, especially certain Indo-Pacific species, feed heavily on corals, whereas various other filefishes find their food from among other elements of the benthos.

Filefishes are recognized as being diurnal. For example, Starck and Davis (1966) described *C. pullus* as resting at night wedged in rocky holes on reefs in Florida.

Family Ostraciontidae: boxfishes

Ostracion meleagris (Shaw)—*pahu*

This boxfish is widespread on nearshore reefs in Kona, but is nowhere numerous, except occasionally in some parts of the boulder habitat. During the day it swims, slowly, close among rocks and coral, now and then picking at the substratum. I saw several in the same places at night, but at the time felt they had been disturbed from resting places by my activity. It was difficult to appraise the nocturnal behavior of this species, owing to its relatively low numbers on the reef and the reduced visibility after dark, and because the few observations were somewhat ambiguous.

Of the six individuals (65: 43-80 mm) collected, one speared within 15 min after sunrise as it swam close to the reef had an empty gut, whereas all five taken under similar circumstances, except later in the day (between late morning and late afternoon) had food throughout the gut. The items in the foregut are listed in Table 69.

CONCLUSION.—*Ostracion meleagris* feeds on benthic invertebrates during the day. Its nocturnal status remains uncertain, although tenuous data indicate relative inactivity after dark.

General Remarks on Boxfishes

Boxfishes in the tropical Atlantic generally are described as active during both day and night (Starck and Davis, 1966; Earle, 1972; Collette and Talbot, 1972). Tunicates, the major prey of *Ostracion meleagris* in Kona, were ranked either

TABLE 69.—Food of *Ostracion meleagris*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Didemnid tunicates	3	42.8	25.68
2	Polychaetes	2	13.0	5.20
3	Algae	2	7.4	2.96
4	Sponges	1	2.0	0.40
5	Pelecypods	1	1.0	0.20
6	Prosobranch gastropods	1	1.0	0.20
7	Copepods	1	0.4	0.08
Also, sand and debris		1	6.0	1.20
	Unidentified fragments	2	26.4	10.56

first or second as prey of three of the five West Indian boxfishes studied by Randall (1967). Furthermore, polychaetes and sponges also were found to be important prey in the Atlantic species just as they are in *O. meleagris* from Kona. In the Marshall Islands, the major foods of *O. cubicus* are mollusks, polychaetes, and algae (Hiatt and Strasburg, 1960).

At least some boxfishes, including *O. meleagris* in Hawaii (Gosline and Brock, 1960; Thomson, 1964), release a substance that is toxic to other fishes. This may give them some immunity from predation, as suggested for some tropical Atlantic species by Randall (1967).

Family Tetraodontidae: balloonfishes

Arothron hispidus (Linnaeus)—*'opu hue, keke*

This solitary balloonfish is widespread on Kona reefs, but is nowhere numerous. In daylight it frequently hovers inactively several meters above the reef, although just as often it swims slowly among the rocks and coral. After dark it continues to swim actively, close to the reef.

Nine individuals (253: 187-332 mm) were speared during day and night. The guts of two were empty: one of these was hovering high in the water column during early afternoon when collected; the other was swimming close among rocks during the hour immediately before first morning light. All of the other seven, taken as they swam close to the reef—five during midday, two during midnight—contained identifiable material, as listed in Table 70. The tunicates taken by this balloonfish include several benthic species, both compound and simple forms; the echinoids are the crushed tests and spines of echinometrids and cidarids; the asteroids are mostly tips of the appendages from *Linckia*.

Generally the items are hard-bodied forms that remain recognizable for a relatively long time after ingestion; nevertheless, material from the two individuals collected at night appeared fresher overall than that from the individuals collected during midday.

In the Marshall Islands, the single *A. hispidus* examined by Hiatt and Strasburg (1960) had fed on much the same material as listed above, except that it also had ingested some living scleractinian corals.

CONCLUSION.—*Arothron hispidus* preys on a variety of benthic invertebrates, especially those having a hard or leathery external covering. Limited evidence indicates it is active during both day and night.

Arothron meleagris (Bloch and Schneider)—*'opu hue, keke*

Like its congener *A. hispidus*, above, the solitary species *A. meleagris* (Figure 41) is widespread on Kona reefs, but is nowhere numerous. It does not hover inactively above the reef during the day as *A. hispidus* often does, and on the few occasions when it was seen at night—always under ledges or in crevices—*A. meleagris* seemed inactive. During daylight it swims slowly among the rocks or corals.

Eleven individuals (221: 146-393 mm) were collected during the day. Of three whose guts were empty, two were speared as they swam close to the reef within an hour after sunrise, and one was taken from a small cave during midafternoon. The remaining eight, taken as they swam close to the reef during midday, all contained identifiable material. Seven of these had taken scleratinian corals (mean percent of diet volume: 43.1; ranking index: 37.71), mostly small chunks of encrusting

TABLE 70.—Food of *Arothron hispidus*.

Rank	Items	No. fish with this item ($n = 7$)	Mean percent of diet volume	Ranking index
1	Tunicates	5	33.7	24.07
2	Echinoids	5	28.1	20.07
3	Ophiuroids	3	13.4	5.74
4	Asteroids	3	8.3	3.56
5	Brachyurans	2	6.4	1.83
6	Sponges	1	2.9	0.41
7	Hydroids	1	2.9	0.41
8	Prosobranch gastropods	1	0.1	0.01
9	Pagurid crabs	1	0.1	0.01
Also, algae		1	0.3	0.04
	Unidentifiable fragments	3	3.8	1.63

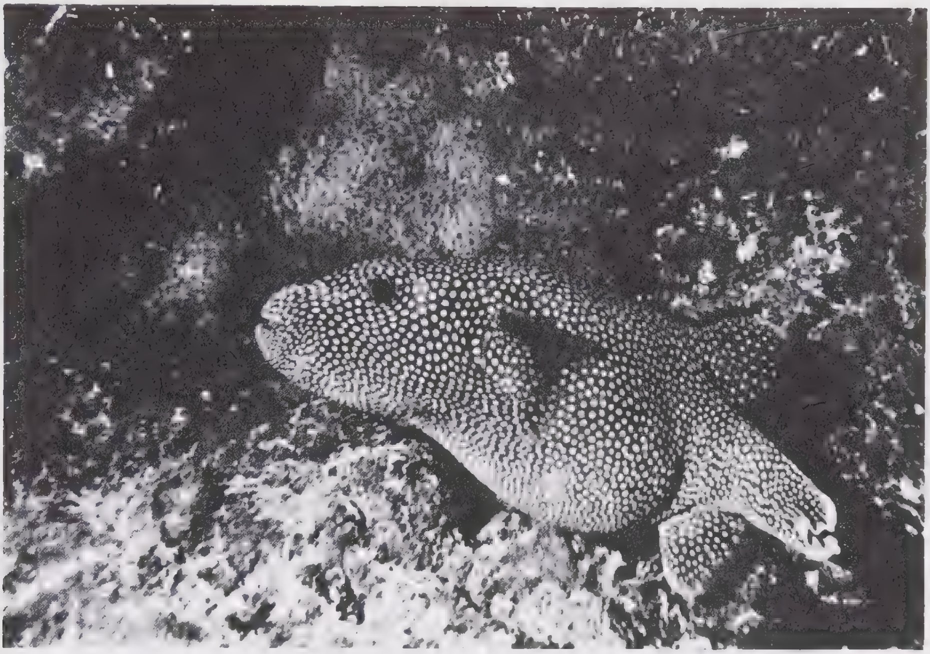

FIGURE 41.—*Arothron meleagris*, a balloonfish. By inflating its saclike body with water, this slow-swimming fish increases its size, which presumably decreases its vulnerability to predators.

Porites, whereas six had taken tunicates (mean percent of diet volume: 44.4; ranking index: 33.3), all of them a large colonial form with a heavy black integument that, like the coral, encrusts on rocks. The only other recognizable items were pectinid pelecypods in one (mean percent of diet volume: 0.6; ranking index: 0.08). Three contained unidentifiable fragments (mean percent of diet volume: 11.9; ranking index: 4.46). Thus, these data indicate that, compared with *A. hispidus*, *A. meleagris* is a relatively specialized feeder. The three *A. meleagris* that Hiatt and Strasburg (1960) examined in the Marshall Islands had fed almost exclusively on living corals.

CONCLUSION.—*Arothron meleagris* is a diurnal predator that feeds mostly on corals and tunicates which encrust on rocks.

General Remarks on Balloonfishes

The dentition of tetraodontids consists of heavy plates, two in each jaw, that form a sharp beak. With this exceptionally strong apparatus, these fishes crush an array of armored organisms that are unavailable as prey to most other fishes (Hiatt and Strasburg, 1960).

Family Canthigasteridae: sharpbacked puffers

Canthigaster amboinensis Bleeker — *pu'u ola'i*

This pufferfish occurs chiefly in relatively shallow water where there is much exposed basalt. It is a solitary fish, active close to the sea floor during the day, but only infrequently in view after dark, when, presumably, it generally retires to reef crevices.

All 11 individuals (69: 31-91 mm) that were speared at various times during daylight contained identifiable material (much of it fresh), as listed in Table 71.

CONCLUSION.—*Canthigaster amboinensis* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied invertebrates.

TABLE 71.—Food of *Canthigaster amboinensis*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Coralline algae	10	42.5	38.64
2	Filamentous algae	8	9.4	6.84
3	Scleractinian corals	6	7.7	4.20
4	Pectinid pelecypods	2	7.8	1.42
5	Brachyurans	2	7.3	1.33
6	Ophiuroids	2	4.9	0.89
7	Echinoids	4	2.4	0.87
8	Sponges	5	1.3	0.59
9	Prosobranch gastropods	4	0.6	0.22
10	Bryozoans	2	0.6	0.11
11	Sipunculid introverts	2	0.3	0.05
12	Foraminiferans	3	0.2	0.05
13	Gammaridean amphipods	2	0.2	0.04
14	Didemnid tunicates	1	0.3	0.03
15	Polychaetes	1	0.2	0.02
Also, unidentified fragments		6	14.3	7.80

TABLE 72.—Food of *Canthigaster jactator*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Coralline algae	3	15.7	7.85
2	Prosobranch gastropods	4	11.2	7.47
3	Sponges	3	6.8	3.40
4	Scleractinian corals	2	10.0	3.33
5	Filamentous algae	5	3.7	3.08
6	Didemnid tunicates	3	6.0	3.00
7	Sipunculid introverts	3	4.3	2.15
8	Echinoids	2	5.5	1.83
9	Bryozoans	2	1.3	0.43
10	Brachyurans	2	1.3	0.43
11	Diatoms	3	0.7	0.35
12	Foraminiferans	2	0.3	0.10
13	Ophiuroids	1	0.3	0.05
14	Ostracods	1	0.2	0.03
15	Gammaridean amphipods	1	0.2	0.03
16	Isopods	1	0.2	0.03
17	Caridean shrimps	1	0.2	0.03
Also, crustacean fragments		1	5.0	0.83
	Sand	3	1.5	0.75
	Unidentified fragments	5	25.6	21.33

Canthigaster jactator (Jenkins)

This small pufferfish lives mostly where corals are well developed. Like its congener *C. amboinensis,* above, it is mostly solitary, although sometimes several occur together. It swims close among the coral during daylight, but is only occasionally in view at night, probably because it usually rests in reef crevices after dark. Once during the predawn hours, as noted above, I observed a nocturnally active moray eel, *Gymnothorax petelli,* grasping one of these puffers between its jaws.

Thirteen individuals (50: 40-70 mm) were speared at various times of day and night. Four were taken during daylight, and these were the only ones that had material in the anterior third of their gut, much of it relatively fresh. In two others taken at night (one 4 h after sunset, the other during the last hour before daybreak), food was confined to the posterior two-thirds of their guts, but much of it was still largely identifiable. In comparison, the remaining seven, collected either at night (more than 4 h after sunset), or during morning twilight, were empty. Items in the six specimens that contained identifiable material are listed in Table 72.

CONCLUSION.—*Canthigaster jactator* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied benthic invertebrates.

Remarks on Sharpbacked Puffers

The canthigasterids are widely recognized as omnivorous fishes that feed on benthic plants and invertebrates (e.g. in the tropical Atlantic by Randall, 1967; and in the western Pacific by Hiatt and Strasburg, 1960). Most investigators have considered them diurnal. Smith and Tyler (1972) described *Canthigaster rostratus* sleeping at night on reefs in the Virgin Islands; Collette and Talbot (1972) also suspected *C. rostratus* to be nocturnally inactive, and suggested that some they saw swimming at night had been disturbed by their lights. To Starck and Davis (1966), however, at least some individuals of *C. rostratus* appeared to be nocturnally active in the Florida Keys; however, they recognized that this species is active in daylight as well.

Family Diodontidae: spiny puffers

Diodon holocanthus Linnaeus — *kokala*

This spiny puffer is numerous in Kona, where it frequently swims close above the reef at night; nevertheless, I never saw one there in daylight. Undoubtedly, it is under shelter during the day, probably deep within the coral caverns that honeycomb much of the reef. In the Gulf of California, where the rocky sea floor offers mostly ledges and relatively shallow caves, one often sees the nocturnally active *D. holocanthus* resting in these places during the day.

All five individuals (211: 175-239 mm) that were speared as they swam in exposed locations on the reef after dark contained identifiable material in their guts, much of it relatively fresh. Prosobranch gastropods, which occurred in all five specimens, were the major food item (mean percent of diet volume and ranking index: 54.1), with pagurid crabs also important prey of all five (mean percent of diet volume and ranking index: 24). Other food items were: echinoids, all *Echinometra mathaei,* in four (mean percent of diet volume: 18; ranking index: 14.4), and ophiuroids in two (mean percent of diet volume: 3.9; ranking index: 1.56). Although this material had been crushed by the powerful jaws and beaklike dentition of the fish, it was apparent that at least many of the gastropod shells actually had housed pagurid crabs; thus the pagurids, not the gastropods themselves, may have been the major food. It remains uncertain how many living gastropods are in fact taken, although opercula among the gut contents showed that living gastropods are important prey.

This circumtropical species has a similar diet in the Atlantic Ocean, as determined by Randall (1967), who also listed prosobranch gastropods as the major food item. He listed pagurid crabs too, but did not suggest that some of the gastropods on his list may have been shells that housed these crabs.

Diodon holocanthus is nocturnal in the Florida Keys, where it stays under ledges or in holes during the day, but emerges at night to feed on various invertebrates, particularly larger shelled forms (Starck and Davis, 1966).

CONCLUSION.—*Diodon holocanthus* is a nocturnal predator that feeds mostly on prosobranch gastropods and pagurid crabs.

Diodon hystrix Linnaeus—*kokala*

During the day, *D. hystrix* either is secreted under ledges, or hovers inactively high in the water column, often several together. At night, solitary individuals (Figure 42) swim in exposed locations close above the reef, especially among basaltic boulders.

Of the 16 individuals (263: 244-333 mm) speared during day and night, only 4 had empty guts, and these were collected during late afternoon, either from holes under rocks, or as they hovered in the water column. The only ones that carried food in the anterior third of their gut were taken at night—two during the hour before midnight and one 2 h before daybreak. Although the anterior third of the gut was empty in the other nine, all carried material posteriorly, which, composing entirely shelled organisms, was readily identifiable: two of these specimens were collected at night—one at midnight, the other just before daybreak; the remaining seven were taken during the day—four of them in the morning, three early in the afternoon. In all, 12 specimens contained identifiable prey.

Echinoids, including both cidarids and echinometrids, occurred in 11 of the 12 specimens and were the major food item (mean percent of diet volume: 55; ranking index: 50.42). Prosobranch gastropods, present in 11 (mean percent of diet volume: 27.1; ranking index: 24.84), were ranked second, and pagurid crabs, also present in 11 (mean percent of diet volume: 12.9; ranking index: 11.83), were ranked third. Thus, the diet includes items similar to those taken by *D. holocanthus,* above, but ranked in a different order. As is true of the material from *D. holocanthus,* many of the gastropod shells had housed pagurid crabs, but the

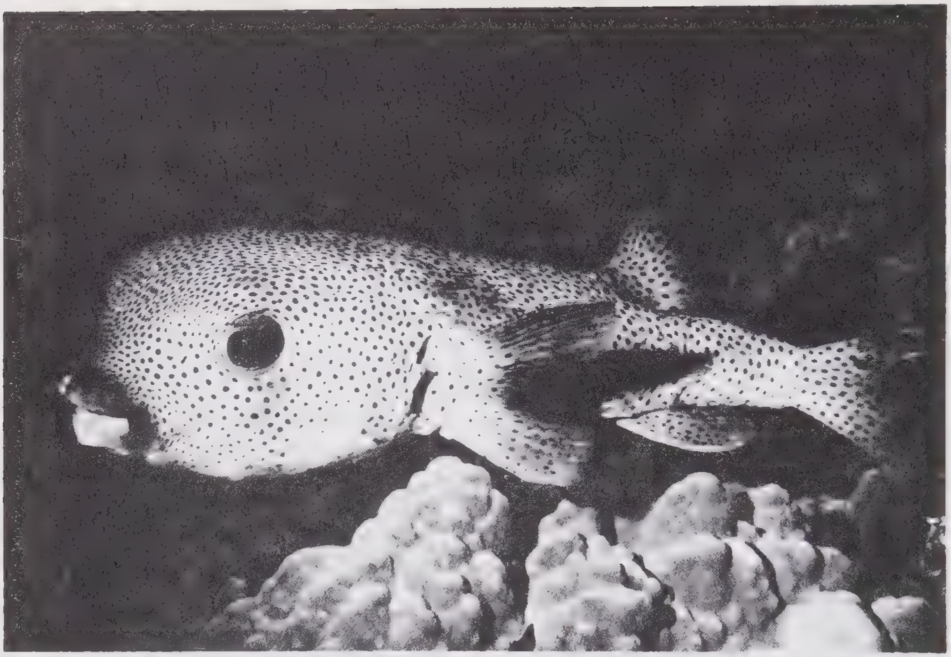

FIGURE 42.—*Diodon hystrix,* a spiny puffer, swimming above the reef at night. With its heavy, beaklike dentition, this fish crushes its shelled prey.

number remains unknown. Nevertheless, the pagurids may actually rank second as prey even though the opercula among this material show that living gastropods are important prey. One *D. hystrix* also contained ostreid pelecypods (mean percent of diet volume: 0.8; ranking index: 0.07), and one contained unidentified fragments (mean percent of diet volume: 4.2; ranking index: 0.35).

Randall (1967) similarly found echinoids the major food of this circumtropical species in the West Indies. For this species as well as *D. holocanthus,* Randall listed gastropods and pagurids separately, without suggesting that some of the gastropods may have been only shells which housed pagurids. Randall recognized that *D. hystrix* feeds partly by night, but believed it to be primarily diurnal. Starck and Davis (1966), however, reported strictly nocturnal habits for *D. hystrix* in the Florida Keys.

The strong, sharp spines that cover *D. hystrix* and *D. holocanthus* are perhaps their most distinctive morphological characteristic. These spines lie flat against their bodies most of the time, but when the bodies inflate with water—a regular response to threats—the spines stand straight out. Although this formidable defense probably deters most predators, the slow-moving *Diodon* would be ready prey for those predators able to tolerate the spines and inflated body. In Hawaii, the tiger shark, *Galeocerdo cuvieri,* regularly preys on full-grown adults of *D. hystrix* (Tester, 1963).

CONCLUSION.—*Diodon hystrix* is a nocturnal predator that feeds mostly on echinoids, and to a lesser extent on prosobranch gastropods and pagurid crabs.

General Remarks on Spiny Puffers

The teeth in both upper and lower jaws of the diodontids are fused together to produce a solid, heavy beak, and this apparatus enables them to crush some of the larger, heavily shelled prey that are beyond the capacity of other fishes—even their relatives the balloonfishes.

The nocturnal habits of the two species of *Diodon,* described above, may be a family characteristic. Starck and Davis (1966) reported that two species of *Chilomycterus* in Florida—*antillarum* and *schoepfi*—are active at night and inactive during the day.

DISCUSSION

The habits of fishes on Kona reefs exemplify the habits of fishes on coral reefs around the world. The following discussion relates these habits to the evolution of fishes on modern tropical reefs, stressing the selective pressures that have shaped the diverse array of forms coexisting on these reefs today. I refer to some of these forms as more advanced, or specialized than others, even though all are products of an equally long evolution, and each is well adaptated to its own specific way of life. Some, nevertheless, have diverged more than others from the generalized carnivores that gave rise to them all, and in this fact lies the basis for the discussion.

The categories erected for presentation have indistinct, overlapping limits, and some species are discussed under one category, rather than another, quite arbitrarily. Nevertheless, the synthesis presented, though an oversimplification, provides a frame of reference within which new information may be assessed. Reemphasizing a point made above, this report deals only with individuals of the various species that behave as adults.

Coral Reefs as a Habitat for Fishes

Most fishes that inhabit coral reefs are among the more recently evolved teleosts (Schaeffer and Rosen, 1961; and others). Indeed, much of the diversity among higher teleosts expresses adaptations to reef habitats. Of the fishes observed along Kona transect lines (Table 7), 98.5% are acanthopterygians.[8]

To properly appreciate the relation of modern coral-reef fishes to their habitat, one should be familiar with the history of tropical reefs. The following outline is based on Newell (1971).

The evolution of tropical reefs can be traced through a fossil record that reaches back into the Precambrian. By the Mid-Ordovician, over 400 million years ago, animal communities had become associated with coral-algal reefs. A succession of reef communities then evolved during subsequent geological history, each with its own characteristic assemblage of animals, and each achieved marked stability before crashing into oblivion during worldwide environmental upheavals. Between each of these periods of stable reef communities, a long time passed without known reefs.

The scleractinian corals, which dominate modern reefs, first appeared during the Triassic, and by Jurassic times, about 150 million years ago, the lithothamnion-scleractinian reef community was well established. Significantly, the teleostean radiation also began during the Jurassic (Gosline, 1971), indicating that their history may closely interrelate with that of the lithothamnion-scleractinian reef community. But Smith and Tyler (1972) suggested that the preacanthopterygian teleosts and their forebearers were maladapted to reef conditions. They contended that fishes entered reef habitats only upon acquiring certain of the morphological advances that marked the first appearance of acanthopterygians early during the Cretaceous, over 100 million years ago. Newell (1971), on the other hand, believed that fishes have had a much longer history as reef inhabitants. He attributed their absence in the fossil record of early reefs to their skeletal remains having been "destroyed by scavengers that abound in this strongly oxidizing environment."

It is unquestioned, nevertheless, that early acanthopterygian fishes—the Beryciformes—were better adapted than were their predecessors for reef habitats. Their increased success probably was based mostly on increased maneuverability and a more adaptive feeding mechanism—the features which Smith and Tyler (1972) felt were especially suited for coral reefs. Patterson (1964) underscored this point when he concluded that most skeletal differences between acanthopterygians and their primitive elopidlike ancestors resulted from changes that permitted the fish better maneuverability: most significant, the fins, given increased rigidity by replacing the anterior soft rays with spines, were more effectively positioned, and the body was shortened and deepened. The advances these fishes made in their feeding mechanism was especially significant, as attested by Schaeffer and Rosen (1961), who stated: "It is primarily the acanthopterygian mouth that has given rise to the enormous variety of specialized feeding mechanisms for which teleosts are so well known. Presumably, the evolution of the acanthopterygian jaw mechanism promoted the successful exploitation of food sources that previously were largely unavailable to actinopterygian fishes." They referred to the protrusible premaxillary of acanthopterygians, which permits them to project their upper jaw at food. Fishes with this mouth construction can accommodate the shape and size of the mouth opening more appropriately to the shape of the food item than can fishes without a protusible premaxillary (Alexander, 1967; Gosline, 1971).

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[8] Because most of the transect counts were made in daylight, there is a bias toward the more advanced forms in numbers of species (the greater incidence of diurnally secretive habits among the more primitive forms, and of diurnally exposed habits among the more highly evolved forms, is discussed below). Even so, however, the preponderance of acanthopterygians is overwhelming, especially if one also considers numbers of individuals. On Kona reefs such advanced groups as the labrids, pomacentrids, and acanthurids are among the species with the largest numbers of individuals. And although among the nonacanthopterygians the numerous muraenid eels are not properly represented in the counts, neither are such nocturnal acanthopterygians as the numerous holocentrids.

During the Cretaceous, in which the beryciforms flourished, the ecological role of the scleractinian corals was challenged by a group of bivalved mollusks, the rudists, which underwent an extraordinary radiation and became the center of a highly successful and widespread reef community. But at the end of the Cretaceous, about 70 million years ago, these and other reef communities collapsed in sweeping extinctions associated with the worldwide biological revolution that marked the close of the Mesozoic (Newell, 1971).

Tertiary seas over most of the world were without known coral-reef communities until lithothamnion-scleractinian reefs underwent a second major radiation during the Eocene, about 50 million years ago (Newell, 1971). The communities that developed in association with these reefs are essentially those of our time. And in what would seem a related phenomenon, the explosive radiation of acanthopterygians into the types that inhabit modern reefs also occurred during the Eocene (Patterson, 1964). Of the families living on reefs today, only a relatively few can be traced back in time earlier than the Eocene (Berg, 1940), and yet by the end of that period, which spanned about 15 million years, representatives of almost every major type of modern fish had appeared (Romer, 1966).

This most recent proliferation of acanthopterygians probably radiated from a line of generalized percoidlike carnivores that had arisen from among the Beryciformes during the late Cretaceous (Gosline, 1966). Above, I note that 98.5% of the fishes seen on Kona transect lines are acanthopterygians; more specifically, 90.4% are acanthopterygians that have reached, or passed, the percoid level of structural development, and 75.5% belong to the order Perciformes (see footnote 7). Only the holocentrids represent the ancestral Beryciformes. In fact, worldwide the Holocentridae, and a few species of Anamalopidae, are the only representatives of this once prolific order that have survived on nearshore reefs.

Obviously the percoid level of development has been highly successful. Gosline (1971) pointed out: "In no single way does it seem to differ from that of the now unimportant, perhaps relic Beryciformes from which it was presumably derived. Possibly the percoids have developed some distinct and as yet unknown biological advantage over the Beryciformes, but for the moment one can only assume that the percoids represent a successful integration of minor advances." The minor advances which Gosline cited include increased maneuverability and adaptability of the protrusible jaw mechanisms, which are refinements on those same features adaptive to reef living that probably gave the Beryciformes an advantage over their progenitors.

Generalized Carnivores: Main Line of Teleostean Evolution

From early Mesozoic times the main line of actinopterygian evolution has progressed through a series of generalized carnivores; with each step forward, the basic feeding mechanism has improved, and the potential for adaptive radiation has increased (Schaeffer and Rosen, 1961). Although this progression has been marked by periodic bursts of specialized offshoots, the primary stem, the generalized carnivore, has remained relatively conservative (Gosline, 1959).

The generalized predator, in simplified form, has a large mouth and is adapted to directly approach, and seize, prey that are fully exposed to the attack. Its prey are small enough to be manipulated, yet large enough to be grasped; moreover, the prey are not sealed in heavy armour, nor do they carry strong spines, spicules, or other noxious components for which the unspecialized digestive tract of the generalized predator is maladapted. Although even the most primitive of today's predators have acquired at least some feeding specializations, the closer one approximates this simplified form, the closer its feeding habits fit this description.

With the generalized predaceous feeding mechanism being a relatively conservative morphological link between periods of adaptive radiation in actinopterygian fishes, one would expect conservative predatory behaviors to be associated with this morphology, and just such behaviors are centered around nocturnal and crepuscular feeding habits. The nocturnal habit involves mostly predation on small, motile crustaceans, the crepuscular habit mostly predation on smaller fishes. Together, crustaceans and fishes are the two major types of prey taken by the generalized predator.

Nocturnal and crepuscular habits among generalized carnivores are discussed separately in the following sections. The separation is artificial, as is the delimitation of a third category, that dealing with generalized carnivores that feed regularly by day. In fact, as illustrated below, the behavior patterns associated with these three types of activity are closely interrelated.

Generalized Carnivores as Nocturnal Predators

Early in the evolving relation between fishes and their prey, the evolutionary lines of many small, vulnerable organisms probably increasingly shifted activity to periods of darkness. There scarcely could be a more elementary solution for animals threatened by active, visually orienting predators. And because effective defense adjustments in prey pressure predators to modify their offense, it seems certain that various predators early aquired means to follow their prey into the night. Thus, in predatory fishes the nocturnal habit itself would be a specialization, but a specialization probably adopted in early preteleostean times that has permitted much of the continued widespread success of the generalized predaceous feeding mechanism.

The smaller generalized carnivores on reefs today find their major prey among the abundant crustaceans, which, as follows from the above, are mostly nocturnal animals that expose themselves at night (Longley, 1927; and others). Many generalized predators that would feed on these organisms have found nocturnal habits adaptive, because only after dark does their straightforward attack find suitable prey in the required exposed position. In this feeding relation, the relatively small size of the crustaceans undoubtedly has influenced the size of the predatory fishes, most of which are of small to medium size (less than about 300 mm long).

Most nocturnal fishes in Kona prey on benthic crustaceans, especially xanthid crabs; however, a number are adapted to take crustaceans and other forms from the water column. The prey of these fishes are mainly relatively large zooplankters (a broad, perhaps loose concept of the term "zooplankton" is used in this report), like crab megalops, that are most abundant in the water column at night. Adults of most nocturnal planktivorous fishes in Kona do not feed significantly on the many small plankters, like calanoid copepods, that predominate in the water column during both day and night.

The extent to which the more primitive reef fishes feed at night seems not properly appreciated. Nocturnal habits are widespread among basal percoids, whereas diurnal habits tend to be characteristic of certain more specialized offshoots. Even if one considers only families that occur in Kona, all nearshore species of the Kuhliidae, Priacanthidae, and Apogonidae seem to be nocturnal, as are many species among the Serranidae, Carangidae, Lutjanidae, Sparidae, and Mullidae.

Probably the nocturnal habits of these more generalized percoids were inherited from ancestral beryciforms. The Holocentridae are the major representatives of this once diverse order on nearshore reefs today, yet as illustrated by their prominence in Kona, they nonetheless are numerous, widespread, and obviously successful. All of them for which there are data are nocturnal, and there is no reason to believe that this is not a primitive characteristic. The anamalopids, which are the only other beryciforms on nearshore reefs, also are nocturnal (e.g. Harvey, 1922). Presumably these modern beryciforms have competed successfully with nocturnal forms among the more advanced teleosts by having refined certain features that are highly adaptive to feeding in the dark. Thus, although much of their anatomy is essentially that of their ancestors, they have acquired highly specialized features—at least many of them sensory—that have permitted more effective use of this equipment. All other present-day beryciforms live in the twilight zone of middepths or in the deep sea, and their suitability to the diminished light of this habitat suggests that their shallowwater ancestors perhaps were nocturnal (Richard H. Rosenblatt, Scripps Institution of Oceanography, pers. commun.). Perhaps during the Cretaceous certain more specialized beryciforms possessed diurnal habits, much as many specialized perciforms do today. But if so, these probably did not survive the widespread extinctions that decimated reef communities at the close of the Mesozoic.

If, as suggested, many reef fishes close to the main line of actinopterygian evolution long ago assumed nocturnal habits in answer to the nocturnal habits of their prey, then one is not surprised to find that widespread predator-prey relations are centered around the nocturnal habit and that the participants are mostly among the more generalized members of the reef community. One especially widespread activity pattern is displayed by the many fishes that assemble in schools on or close to nearshore reefs during the day, then disperse at nightfall and feed on small organisms that become exposed after dark. This is the basic activity pattern of many carangids, lutjanids, pomadasyids, and sciaenids—all among the more generalized perciforms (Hobson, 1965, 1968a, 1972, 1973).

In addition to these basal percoids, it is significant that of the relatively few fishes of preacanthopterygian groups associated with modern reefs, many either follow this pattern themselves, or closely relate as predators to other fishes that do (see next section). A diurnally schooling-nocturnally active pattern is especially widespread, if not universal, among the inshore clupeids, order Clupeiformes—as described earlier for *Harengula thrissina*, an exceedingly numerous fish close to shore in the Gulf of California (Hobson, 1965, 1968a). Starck and Davis (1966) found this same pattern in all five clupeids that they studied on reefs in Florida, and I observed it in *Herklotsichthys punctatus* in the Marshall Islands (unpubl. data). Pertinent information on nearshore clupeids is limited because so few investigators have distinguished between diurnal and nocturnal activity; nevertheless, there are at present no data refuting the generalization that these fishes feed at night.

There are fewer of these diurnally schooling, nocturnally active fishes on Kona reefs than on most other tropical reefs, perhaps for reasons discussed earlier (Hobson, 1972). Still, the pattern is well defined there in certain of the mullids, genus *Mulloidichthys,* and in the lutjanid *Lutjanus vaigiensis,* and is especially apparent in the atherinid *Pranesus insularum,* just as in its congener *P. pinguis* of the Marshall Islands (Hobson and Chess, 1973)—both of the preacanthopterygian order Atheriniformes.

Generalized Carnivores as Crepuscular Predators

In the same way that many generalized predators are nocturnal because suitable prey are most available to them after dark, other generalized predators—those that prey mostly on smaller fishes—are primarily crepuscular because that is when these prey become most vulnerable to their mode of attack (Hobson, 1968a). Moreover, just as is true of the nocturnal forms, the crepuscular piscivores, which also are among the more generalized of the reef fishes, experience certain long-established predator-prey relations. Significantly, many of these crepuscular piscivores are members of the same basal percoid families, the Serranidae, Carangidae, and Lutjanidae, that have produced some of the nocturnal predators discussed above. Many of the crepuscular piscivores, however, tend to be larger than the nocturnal species, which might be expected, inasmuch as the nocturnal fishes are among their major prey (Hobson, 1968a). Schools of nocturnal carangids, pomadasyids, mullids and, especially, clupeids, are well-known targets of such piscivores.

During the twilight periods of greatest piscivorous activity (Hobson, 1968a, 1972), these nocturnal fishes are still in their diurnal schools. And although the schools effectively protect them from predators during most of the day (Manteifel and Radakov, 1961; Eibl-Eibesfeldt, 1962; Hobson, 1968a), this protection is reduced during twilight (Hobson, 1968a). At this time of maximum danger from predators, most other smaller reef fishes, both diurnal and nocturnal, are under cover; thus, the schooling fishes, which are still in the water column, become the most numerous prey of proper size exposed to the space-demanding attacks of the generalized piscivores (Hobson, 1968a). After dark, the smaller fishes seem relatively safe from at least most such predators (Hobson, 1973), but during the changeover between day and night, they are vulnerable (Hobson, 1968a; Munz and McFarland, 1973).

The large piscivores are exceptionally abundant in certain parts of the Gulf of California where the diurnally schooling, nocturnally active fishes are numerous (Hobson, 1968a). As suggested earlier (Hobson, 1972), the relatively few such large predators on Hawaiian reefs, compared with most other tropical areas, may relate to the relative dearth in Hawaii of schooling prey.

Thus, a major activity pattern of these large piscivores closely interrelates with a major activity pattern of the smaller nocturnal predators. For this reason, and because so many members of the two groups are closely related taxonomically, it is apparent that the crepuscular pattern probably has had a longevity comparable to that of the nocturnal pattern. A good indication of this long history exists in the Gulf of California, where the day-night activity pattern of the nocturnal clupeid *Harengula thrissina* closely interrelates with the crepuscular activity not only of certain basal percoids, but also of *Elops affinis,* order Elopiformes, a member of the most primitive of all extant teleostean genera (Hobson, 1968a).

Generalized Carnivores as Diurnal Predators

Thus, nocturnal or crepuscular habits are adaptive for many generalized carnivores. Others with basically the same feeding mechanism, however, have acquired morphological and behavioral characteristics suited to capture small, motile crustaceans and, especially, fishes in daylight. Despite the fact that crustaceans are most exposed to direct attacks at night, and smaller fishes generally are most vulnerable to such attacks during twilight, various predators are equipped to exploit the exceptions to these generalizations.

True, selective pressures applied by generations of visually orienting predators have refined the defense mechanisms that protect so many prey organisms during daylight. But there are occasional lapses in all these defenses when the prey are briefly vulnerable. For example, nocturnal organisms resting under a thin layer of sand occasionally betray their presence by moving. And small fishes that usually are within retreating distance from cover sometimes stray too far into the open; or others, enjoying the security of a school, occasionally drift too far from their fellows. Still others, normally alert to surrounding danger, are momentarily distracted. At such times, these organisms are open to attack. But normally such events fail to occur in the presence of large, free-swimming predators that are actively hunting. Potential prey are sensitive to cues that mark the hunting predator, and take defensive action when a hunter appears—cryptic forms stop moving, others move closer to cover, and schooling forms draw themselves closer together (Hobson, 1965, 1968a). Above all, in this alerted state the prey are less likely to make a defensive mistake. This does happen occasionally, of course, as when large carangids swim slowly among schooling prey for hours during the day without an aggressive move, and then suddenly attack —presumably having sensed a vulnerable target (Hobson, 1968a). Probably this offensive tactic depends on the prey eventually becoming conditioned to the predator's presence, and finally making a mistake. But it seems unlikely that such predators could depend on these relatively infrequent successes. They remain best suited for crepuscular attacks.

The problem of being within striking range when prey are momentarily available during the day because of a defensive lapse is probably best solved by those predators that lie in wait under concealment—the ambushers—or by those that stalk. Both tactics have produced some highly specialized forms that are more appropriately considered in the next section. However, many of those that use concealment to ambush their prey look much like the nocturnal or crepuscular predators discussed above, and so are considered here.

This is especially true among certain basal percoids, like the serranids. For example, many species of *Epinephelus* ambush prey from a concealed position, and much of this activity occurs in daylight (Hiatt and Strasburg, 1960; and others). Most of these predators are cryptically hued for a sedentary existence among rocks or coral— usually they are brown or grey, with the hues often arranged in blotches or spots. Such predators rest unseen until a small organism within striking distance makes a defensive error.

Generalized predators adapted for this tactic are well known to feed regularly during both day and night, as exemplified by certain species of *Epinephelus* (Longley and Hildebrand, 1941; Starck and Davis, 1966; Hobson, 1968a). There is evidence, however, that feeding habits of these predators differ between day and night. In the Gulf of California, *E. labriformis* preys almost entirely on crustaceans at night, but heavily on fishes during the day (Hobson, 1968a). I have already commented on the increased vulnerability of small crustaceans at night; apparently fishes are more vulnerable to the predatory tactics of this fish in daylight. The diurnal piscivorous habit of *Cephalopholis argus* (*Epinephelus argus* of some authors, e.g. Smith, 1971) in Kona is consistent with this probability.

Predators having obvious morphological and behavioral specializations that increase their proficiency as ambushers or as stalkers are considered in the next section.

Specialized Offshoots from the Main Line of Teleostean Evolution

Most fishes inhabiting tropical reefs today, as exemplified by species in Kona, represent specialized offshoots from the main teleostean line.

Predators Specialized to Ambush Prey

As emphasized in the introductory remarks, the categories erected in this discussion overlap. This is especially true of predators that ambush their prey. By using this tactic, predators with the generalized feeding mechanism increase their capacity to capture prey in daylight. But many ambushers, like certain species of *Epinephelus,* are so similar in both morphology and habits to many of the nocturnal and crepuscular forms discussed above that one can only arbitrarily distinguish them as being specialized in this activity. Nevertheless, some forms have retained the generalized feeding mechanism while diverging widely from the primitive form in other respects. And the divergence is based on features that better adapt these fishes for the ambushing tactic.

The synodontids, order Myctophiformes, which are prominent ambushers in Kona, as they are on most other tropical reefs, are products of an evolutionary offshoot that diverged from the main line at a preacanthopterygian level. Thus, the ambushing tactic has had a long history. The scorpaenids, order Scorpaeniformes, and the bothids, order Pleuronectiformes, both of whose Kona representatives include specialized ambushers, belong to groups that diverged from the mainstream near the percoid level (Gosline, 1971; and others). Significantly, the adults of all these forms seem to be primarily piscivorous during the day.

The synodontids, scorpaenids, and bothids that ambush their prey have acquired characteristics that camouflage them as they lie on the sea floor. Clearly, it is important for these predators to go unseen by their victims. In this respect, many of the cirrhitids, order Perciformes, might seem a puzzle. An example from Kona is *Paracirrhites forsteri* (Figure 32), which preys mostly on smaller fishes during the day. Although attacking prey in much the same manner as other ambushers, this colorful fish is clearly visible as it rests in exposed positions on the reef. Selection, in this case, may have in fact favored coloration that attracts attention. Conceivably this could be an effective offensive characteristic, just so long as its use among predators is limited. It is well known that certain small fishes are attracted to conspicuous objects on the sea floor—one needs only to place a small, shiny artifact on the bottom to see this. Perhaps *P. fosteri* actually finds prey among small fishes that approach to investigate its conspicuous features.

Predators Specialized to Stalk Prey

Many predators specialized to stalk prey in the water column belong to groups whose ancestors diverged from the main teleostean line below the percoid level. Characteristically, they have long, attenuated bodies. Among species whose behavior in Kona is described above are the trumpetfish, *Aulostomus chinensis*, and the cornetfish, *Fistularia petimba*—both of the order Gasterosteiformes.

Two other highly specialized stalkers on Kona reefs were not included in the species accounts above because observations on them were infrequent; these are the needlefish, *Strongylura gigantea,* order Atheriniformes, and the barracuda, *Sphyraena barracuda,* order Perciformes. The various species of needlefishes and barracudas are widespread on tropical reefs, and their stalking habits are well documented. Hiatt and Strasburg (1960) reported that *Strongylura gigantea* feeds on small fishes in the Marshall Islands by "drifting up to them and suddenly lashing out with its jaws." On the basis of similar observations in the tropical Atlantic, Randall (1967) reported that needlefishes are almost exclusively piscivorous, and that they "drift slowly into range of one of their prey before making a quick rush." Regarding barracudas, Hiatt and Strasburg (1960) told of *Sphyraena genie* in the Marshall Islands "drifting solitary near the surface stalking its prey" and stated that "it surprises its victim with a sudden lunge." Randall (1967) noted that barracudas in the tropical Atlantic feed primarily on fishes during the day, a statement probably true of at least most stalking predators.

Predators Specialized to Seek Prey in Reef Crevices

Here I am concerned primarily with muraenid eels, order Anguilliformes, and the brotulids, order Gadiformes. Members of both groups, but the eels in particular, have elongated bodies suited to maneuvering through the crevices that honeycomb coral reefs. Their similar morphologies led early Hawaiians to group eels and brotulids together by the generic term *puhi*. There are a number of other secretive forms on Kona reefs—small inconspicuous fishes like the pseudochromid *Pseudogramma polyaccanthus*, which were occasionally visible at night during this study—but because I have little knowledge of their habits they are not considered here.

The muraenid eels are products of an evolution that has diverged widely from the main teleostean line: today they possess many specialized features that equip them for hunting in reef crevices. The primary specializations, for example their exceptionally solid skulls, are adaptive for wedging through small openings, and they can back out of any hole they enter (Gosline, 1959, 1971). Many of the morays, and at least some of the brotulids, for example *Brotula multibarbata* in Kona, are nocturnal; however, other morays are diurnal. Obviously hunting conditions in reef crevices differ between day and night.

Reef crevices are havens for numerous creatures. Many diurnal forms rest there at night, some of them virtually asleep, and many nocturnal forms shelter themselves there in daylight (Hobson, 1968a, 1972). Moreover, most reef animals find refuge in these crevices when they are injured or distressed; obviously, sheltering in reef crevices is adaptive for prey threatened by the many predators on the surface of the reef. But it is equally obvious from their long successful history on tropical reefs that eels have acquired adaptive means to exploit such prey.

Predators with Sensory Specializations That Detect Concealed Prey

In this category I am concerned with the mullids, order Perciformes, which are prominent on Kona reefs. Their distinctive sensory chin barbels permit them to locate prey that go undetected by other fishes. And, like the muraenid eels, above, their numbers include both diurnal and nocturnal forms, as well as species that hunt effectively during both day and night. This fact, and the great diversity in their prey, shows that mullids, with their distinctive modes of feeding, have available to them a broad range of predatory activity denied most other fishes.

Although seeking refuge under rocks, algae, or sand is adaptive for many small animals approached by a predator, this tactic probably plays to the advantage of some mullids. For example, the diurnal *Parupeneus chryserydros* preys mostly on small diurnal fishes that typically take cover when threatened. This mullid may use its exceptionally long barbels not only to locate such animals, but also to drive them into the open.

Many small organisms that seek cover when threatened rest in the same refuges when they are inactive, and at such times may be prey for other mullids, notably *P. bifasciatus*. This species seems to feed with equal effectiveness day and night, although its food habits differ between these two periods. In this respect, a comparison with the serranid *Epinephelus labriformis* in the Gulf of California is insightful. As noted above, *E. labriformis* also feeds regularly day and night, taking mostly crustaceans after dark and small fishes in daylight; thus, its food habits agree with the generalization that crustaceans are most vulnerable at night, and fishes most vulnerable in daylight. *Parupeneus bifasciatus* seems to be a successful exception to this generalization, because it takes fishes more often at night than during the day and crustaceans more during the day than at night. Apparently, *P. bifasciatus* is specialized to capture prey that rest under cover, safe from predators with generalized feeding equipment.

Thus, at least some mullids find prey among animals that have sheltered themselves in the reef, just as do some of the muraenid eels, so that, like the eels, they have gained advantage from what generally are successful defensive behaviors in their prey. But whereas the eels probe deep into reef interstices, the mullids confine their activity to the superficial covering on the reef.

Predators Specialized to Take Prey Among the Plankton During the Day

There are clear distinctions between diurnal and nocturnal planktivorous fishes on coral reefs, with the diurnal species inactive at night and the nocturnal species inactive during the day (Hobson, 1965, 1968a, 1972; Starck and Davis, 1966). Emery (1968) showed that the composition of plankton over reefs in Florida also differs between day and night, a fact undoubtedly related to the diurnal-nocturnal dichotomy among the planktivorous fishes. As described above, planktivorous fishes that feed in the water column at night, for example *Myripristis* and *Apogon,* have the generalized carnivore's large mouth and prey largely on the relatively large plankters, like crab megalops, that are mostly in the water column above the reef after dark.

Although a large array of plankters inhabit the water column during the day, generally they seem too small for adults of the large-mouthed nocturnal planktivores. Significantly, diurnal planktivores all have a small mouth, and their major prey, calanoid copepods, are generally smaller than the prey of their nocturnal counterparts. Moreover, diurnal planktivores among adult reef fishes generally are among the more advanced teleosts, having attained, or passed, the percoid level of development. There are no basal percoids among the prominent diurnal planktivores in Kona, but in the tropical Atlantic certain serranids, lutjanids, and pomadasyids specialized in this habit are numerous (Starck and Davis, 1966; Randall, 1967). Most diurnal planktivores on coral reefs, however, are among the higher Perciformes. These include the pomacentrids, which probably include a higher proportion of planktivorous species than any other major family of coral-reef fishes. The balistids, order Tetraodontiformes, are among the most advanced teleosts and include several specialized diurnal planktivores: species of *Melichthys* and *Xanthichthys ringens* are prominent on coral reefs over much of the tropical world.

Many unrelated species that forage on zooplankton in the water column during the day display convergent morphologies. Features characteristic of these fishes were identified by Davis and Birdsong (1973), who did not distinguish between diurnal and nocturnal forms, however. Drawing examples from the tropical Atlantic Ocean, they illustrated certain unrelated planktivorous fishes, for example *Paranthias furcifer* (a serranid) and *Chromis cyanea* (a pomacentrid), that, on casual inspection, look more like one another than they do members of their own families that feed on the benthos. The similarity among these unrelated forms is based mainly on their common increased tendency toward a fusiform body, a deeply incised (forked or lunate) caudal fin, and a small, upturned mouth that gives their heads a characteristic appearance. Presumably diurnal planktivores that tend toward a more fusiform body and deeply incised caudal fin—both well-known characteristics of rapid-swimming oceanic fishes—can swim faster than relatives in which these tendencies are less developed. Considering the many active predators at large during the day, increased speed clearly is adaptive for small reef fishes that swim at that time in open water, high above the sheltering reef. The advantage of the upturned mouth may be indirect: Rosenblatt (1967) acknowledged Walter A. Starck II for pointing out that this mouth construction gives the fish a shortened snout, which permits close-range binocular vision—an obvious advantage in capturing tiny organisms in the water column. A number of diurnal planktivorous fishes in Kona possess one or more of these characteristics, as described and illustrated above (e.g. Figures 38 and 40).

Significantly, none of the nocturnal planktivores in Kona tend toward having either a more fusiform body, or a more deeply incised caudal fin. In fact, planktivorous squirrelfishes of the genus *Myripristis* are actually deeper bodied than their bottom-feeding relatives of the genus *Holocentrus,* and the caudal fins of most are less deeply incised (compare, for example, Figures 11a and 14). If, as suggested above, these features gain selective advantage in the planktivores by providing added speed to elude predators in open water, then their absence among forms that rise into the water column after dark is consistent with the contention (above, and Hobson, 1973) that small free-swimming fishes face a much diminished threat from predators at night. Many of the nocturnal species, including species of *Myripristis,* have the sharply upturned mouth; but it is a large structure, as noted above, suited to taking the larger zooplankters that appear in the water column after dark.

Not all of the diurnal planktivores in Kona tend toward fusiform bodies, deeply incised caudal fins, or sharply upturned mouths. None of these features occur in the planktivorous chaetodontids, for example *Hemitaurichthys zoster* (Figure 28a), which nevertheless are well suited to feed on copepods, and other tiny zooplankters in the water column by day. Obviously many conflicting pressures have differentially affected the morphologies of the various fishes that forage on tiny organisms in the mid-waters.

Predators Specialized to Prey on Benthic Invertebrates During the Day

A wide variety of fishes prey on benthic invertebrates during the day. They include most of the labrids, chaetodontids, balistids, canthigasterids, monacanthids, ostraciontids, and tetraodontids, as well as many of the pomacentrids, blenniids, and others—all of them higher perciforms or tetraodontiforms. Their prey are among the more prominent invertebrates on the reef, including such sessile forms as sponges, coelenterates, and tunicates; and also various slow moving animals like echinoids and gastropods. Typically, these prey are fortified with toxic or noxious components, like spines, spicules, nematocysts, or tough, fibrous components; or they are encased in heavy armour. Because of these defensive features, fishes that prey on such forms must have specialized feeding structures or techniques—the unspecialized feeding apparatus of generalized predators is maladapted for this task. Also unavailable to generalized predators are the many very small organisms whose capture requires delicate manipulations or movements for which large-mouthed fishes are unsuited. Moreover, many of these prey are diurnally cryptic or secretive, thus requiring still additional specializations to capture them in daylight.

Thus, fishes that successfully feed on most benthic reef invertebrates during the day are advanced species whose evolution has been mostly one of perfecting means to feed in daylight on prey that are beyond the capacity of fishes with generalized feeding equipment. Certain mullids, discussed above, are adapted to feed on many of these prey, but mullids use nonvisual means, whereas fishes considered here are primarily visual feeders.

These are fishes that have passed the percoid level of development. The evolution of the percoid morphology, especially with its highly adaptive feeding mechanism, gave fishes added potential to adjust to a wide variety of feeding situations. But although percoids appeared first during the Cretaceous (Patterson, 1964), not until modern reef communities appeared during the Eocene (Newell, 1971) does it appear they began to fully realize this potential.

Bakus (1964, 1966, 1969) concluded that the secretive habits and defensive structures of many benthic invertebrates on coral reefs today, including sponges, didemnid tunicates, and others, are the result of predation pressures from fishes. Whether or not this is so, certainly the array of specialized feeding habits and structures that characterize diurnal bottom-feeding fishes on coral reefs are mostly adaptations which cope with specific defensive characteristics of their prey. Because predation pressures lead to defensive adjustments in prey, and these in turn stimulate further offensive modifications in predators, it is not surprising that the diverse array of defenses in benthic invertebrates today is matched in the fishes that feed on them by an equally diverse array of solutions. These solutions to invertebrate defenses are manifest in the extremely varied feeding structures and behaviors that occur among diurnal fishes. Most diurnal fishes specialized for diets of benthic invertebrates have relatively small mouths, but beyond this their feeding morphologies have diverged widely.

Sessile invertebrates seem to be significant prey only during the day, perhaps because an animal must move to be sensed by most predaceous fishes at night (Hobson, 1968a). Thus, the few highly specialized fishes that feed on sponges are strictly diurnal. In Kona, the chaetodontid *Holacanthus arcuatus* feeds on some of the larger sponges that encrust in exposed locations on rocks, whereas the zanclid *Zanclus canescens* uses its elongated snout to feed on some of the smaller sponges that are attached within crevices or depressions on the reef. Randall and Hartman (1968), in studying sponge-feeding chaetodontids and monacanthids in the West Indies, noted that sponges cannot be digested by most fishes, and concluded that these organisms have become available as food for only a few highly specialized teleosts in geologically recent times.

Some diurnal predators, for example *Forcipiger flavissimus, Chaetodon auriga,* and *C. fremblii,* among chaetodontids in Kona, habitually tear off pieces of larger sessile invertebrates, including polychaetes, tunicates, and alcyonarians. The analogy drawn above between the snout and jaws of *F. flavissimus* and a pair of needle-nosed pliers underscores the suitability of this fish's feeding morphology for its feeding habit.

One of the most obvious potential foods for carnivorous bottom-feeding fishes on coral reefs would seem to be the corals themselves. Nevertheless only some of the most advanced teleosts exploit this resource. In Kona, coral eaters include certain chaetodontids, pomacentrids, and blenniids (all higher Perciformes) and certain monacanthids and tetraodontids (all Tetraodontiformes). In pointing out that coelenterates are not food for fishes in most marine communities, Hiatt and Strasburg (1960) cited various specialized features of fishes that prey on corals in the Marshall Islands: for chaetodontids and monacanthids that snip off individual polyps, they listed the produced snouts, small terminal mouths, and fine protruding incisiform teeth; for tetraodontids and balistids that bite off larger pieces of coral, they noted very heavy, strong dentition. All fishes that feed on coral, including those that feed heavily on coral mucus, seem to be diurnal. Obviously a predator that bites off large chunks of coral, or which scrapes away mucus, would find diurnal habits adaptive—its food is equally accessible day or night, and its own activity would benefit from daylight. On the other hand, the polyps of some coral species are most expanded at night, suggesting that perhaps predators that would snip them off might find them most accessible after dark; however, the precise manipulations involved in this activity probably require the light of day, because without exception all such predators are diurnal.

Daylight and precise manipulations also seem required of predators that pluck tiny cryptic organisms, notably amphipods, from amid benthic cover. An example from Kona is the labrid *Anampses cuvier,* whose prey are amphipods and other organisms too small for large-mouthed generalized predators of comparable size. Taking such prey requires a specialized tactic and feeding mechanism. Characteristically such predators hover within a few centimeters of the substratum, inspecting the surface. When they spot prey —perhaps through movement or an unusual contour—they take it in a characteristic plucking manner.

Probably this way of plucking tiny prey from a substratum preadapted precursors of those fishes that are specialized as cleaners. Most cleaner fishes, which include certain labrids, pomacentrids, and chaetodontids, pluck various materials, mostly ectoparasitic crustaceans, from the bodies of other fishes. Possessing both the necessary techniques and morphology, certain fishes in this category were prepared to adopt the cleaning habit when their concept of a suitable feeding substratum broadened to include the bodies of other fishes (Hobson, 1971). A few species, like *Labroides phthirophagus* in Kona, are specialized as cleaners, having refined both their feeding morphologies and techniques to more efficiently practice this habit. All known cleaner fishes are diurnal.

Most of the invertebrate prey of diurnal fishes are insignificant as prey of nocturnal fishes. However, the specializations that permit certain diurnal fishes to seek out secretive prey in daylight make available to them at that time some of the forms—motile crustaceans in particular—that are important prey of various generalized predators after dark. For some fishes, the adaptations that permit them to take crustaceans and other forms from under reef cover in daylight are morphological. Thus, the chaetodontid *Forcipiger longirostris* and the labrid *Gomphosus varius* both have elongated snouts with which they reach deep into reef crevices for crustaceans. In other fishes the adaptations that make secretive prey available are more strictly behavioral. Thus, the labrid *Thalassoma duperrey* follows close to the feeding jaws of large herbivores and other fishes that disturb the substratum, and snaps up tiny crustaceans driven from cover. This behavior is widespread, occurring in other wrasses in Kona and also in the Gulf of California (Hobson, 1968a). Some species lower on the evolutionary scale seem to have similar behavior: as suggested above, the carangid *Caranx melampygus* may enjoy this advantage by following the mullid *Parupeneus chryseydros,* as may the aulostomid *Aulostomus chinensis* by accompanying grazing schools of acanthurids—in these two situations, however, the prey seem to be mostly small fishes.

Some diurnal predators excavate buried prey, as when the labrid *Coris gaimard* overturns small stones with its snout and feeds on animals thus exposed. And in the eastern Pacific the balistid *Sufflamen verres* uncovers prey buried in the sand by exposing them with a jet of water from its mouth, or by rapidly undulating dorsal and anal fins while lying on its side, thereby generating currents that sweep the sand away (Hobson, 1965, 1968a). Similarly, the ostraciontid *Lactophrys triqueter* in the tropical Atlantic by jetting water from its mouth uncovers prey buried in the sand (Longley, 1927).

Related Problems of Species Recognition.—The enormous potential for varied feeding adaptations in these advanced teleostean groups has led to the occurrence on most coral reefs of large numbers of closely related species that seem to have diverged from one another chiefly on the basis of differing food habits. For example, 14 species of the genus

Chaetodon occur together on Kona reefs—all very similar in general body form, but with distinctive differences in diet and related morphology. Obviously, such situations can exist only if, in addition to having acquired adaptations suited to specialized diets, closely related forms have also acquired effective barriers to interbreeding. Central to this is the ability of each individual to recognize others of its own kind, which probably relates to the circumstance that most species in this category have highly visible species-specific color patterns.

It is logical that diurnal fishes would employ visual cues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona tend to accentuate a contrast, thus making them more visible at lower light levels (e.g. Figures 28a and b; 29a and b). Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder, 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display. This phenomenon appears most pronounced among fishes in the present category, but others show it as well; for example, in Kona certain of the nocturnal squirrelfishes, *Holocentrus* (Holocentridae: Beryciformes) display characteristic white bars or spots at night that are more visible under reduced light than their daytime colorations would be (e.g. Figure 12a and b). Probably one can generalize only to the extent that distinctive day/night colorations in coral reef fishes reflect distinctive day/night situations.

Fishes Specialized to Feed on Vegetation

Vegetation, which carpets much of the rocky sea floor inshore, would seem ready food for fishes. Yet relatively few species utilize this resource, even though, as in Kona, they often predominate on tropical reefs. The herbivorous habit is an advanced trait among marine fishes, a fact recognized by Hiatt and Strasburg (1960).

In general, herbivorous fishes on coral reefs share many characteristics with the diurnal predators that are specialized to prey on benthic invertebrates, discussed in the previous section. Like the fishes grouped together in that category, at least most coral reef herbivores are active by day and relatively inactive at night; furthermore, they too tend to be colorful animals that have small mouths which are part of highly evolved feeding systems. In fact, several families of fishes span both categories; for example, the Chaetodontidae, Pomacentridae, Blenniidae, Balistidae, Monacanthidae, and others include gradations of species from some that are strictly carnivorous, to others that feed on both plants and animals, to still others that are strictly herbivorous. Within these groups, which have favored plasticity in feeding habits and structures, it seems that characteristics adaptive to plucking benthic invertebrates from the sea floor have been modified in some species for grazing on plants.

Nocturnal Activity Among Advanced Teleosts

Not all the more advanced fishes are diurnal. The chaetodontid *Chaetodon lunula* seems to be nocturnal in Kona, and at least some of its congeners—notably *C. quadrimaculatus* and *C. auriga*—may feed to some extent after dark. But these are exceptional cases in an overwhelmingly diurnal group. As suggested above, nocturnal activity in these instances may relate to competition among the exceptionally large number of *Chaetodon* species that cooccur on Kona reefs.

Nocturnal habits cannot be regarded as exceptional where they occur among the diodontids, however, because night feeding seems to be the rule in this family. And these members of the order Tetraodontiformes are among the most highly evolved of all reef fishes. The prey of *Diodon hystrix* and *D. holocanthus* in Kona —large echinoids, gastropods, and pagurid crabs—are more exposed at night than during the day. And because they are relatively large and move at least intermittently after dark, one can predict they would be suitable quarry for nocturnal predators having means to crush heavy armour. These are large prey, so a predator must carry its crushing mechanism in its mouth, rather than in its throat—as do many of the labrids and other predators that feed on smaller mollusks and echinoids during the day. The highly evolved diodontids accomplish this job with their powerful crushing jaws, but the problem has also been solved at a more primitive level by certain basal percoids. In Kona, the nocturnal sparid *Monotaxis grandoculis*, with its molariform dentition, has feeding habits similar to those of the diodontids, but with less emphasis on heavily armoured forms. Clearly, the diodontids, with more powerful jaws and heavier dentition, are better adapted than the sparids for this particular task. Of even more primitive stock than the sparid, the muraenid eel *Echidna zebra* has crushing dentition, but its prey seem to be primarily large crabs that it takes regularly from reef crevices in daylight. There is no evidence that it can crush the heavy gastropods so prominent in the diets of the more advanced sparids and diodontids.

CONCLUSIONS

1. The feeding relationships of fishes on coral reefs in Kona, Hawaii, follow essentially the same pattern as do feeding relationships of fishes on coral reefs elsewhere.

2. Nocturnal habits have had a long history in teleostean fishes, and are widespread among the more generalized forms, including many of the clupeids, holocentrids, serranids, kuhliids, priacanthids, apogonids, lutjanids, and others. These large-mouthed predators find night feeding adaptive because that is when their prey—mostly small, motile crustaceans—are in exposed locations and thus vulnerable to their straightforward attack.

3. Piscivorous predators that have a generalized feeding mechanism, and which attack with a straightforward charge, for example certain large carangids, are mostly crepuscular.

4. Certain piscivorous predators that have a generalized feeding mechanism feed effectively during the day, as well as during twilight, by ambushing or stalking their prey. The ambushers, which include certain synodontids, serranids, scorpaenids, and bothids, typically have cryptic morphology, coloration, and behavior. The stalkers, which include the aulostomids, fistulariids, belonids, and sphyraenids, typically have long, attenuated bodies.

5. In acquiring features adaptive for hunting in reef crevices, muraenid eels have become highly successful, capitalizing on the otherwise effective shelter-seeking habits of small reef animals. Although many small reef animals become more vulnerable to eels when they shelter in reef crevices, they find these refuges adaptive when resting, injured, or distressed, because they are relatively safe here from the even greater threat from predators that exists on the surface of the reef.

6. The mullids use their distinctive sensory barbels to locate prey that are sheltered under the superficial covering of the reef and adjacent sand. Some mullids are best adapted to capture such prey at night, others to capture such prey in daylight, and some feed effectively during both day and night. At least some use their barbels not only to detect prey, but also to drive them into the open.

7. Most fishes on Kona reefs, like fishes on coral reefs elsewhere, are among the more recently evolved teleosts, having reached, or passed, the percoid level of structural development.

8. The adaptability of the perciform feeding apparatus has given rise to a wide variety of forms that have diverged from one another primarily on the basis of differing food habits. Much of this diversity has resulted from adaptations that cope with specific defensive characteristics of the organisms on which these fishes feed.

9. Just as nocturnal and crepuscular habits predominate among the more generalized coral-reef fishes, diurnal habits predominate among the more advanced, specialized forms, including most of the higher Perciformes, and Tetraodontiformes. Some of the most advanced of all, however, including the diodontids, are nocturnal.

10. Some higher teleosts, including certain chaetodontids, labrids, and balistids, have specializations that permit them to capture, during daylight, nocturnal forms hidden under cover. Such prey include forms like motile crustaceans that expose themselves at night, and at that time become the major prey of generalized nocturnal fishes.

11. Some advanced teleosts, including certain chaetodontids, labrids, and pomacentrids, are specialized to pluck tiny prey, such as amphipods, from among vegetation and other benthic cover. These prey are too small, and too cryptic, to be taken after dark or by predators with a large mouth. This plucking habit preadapted certain species for cleaning ectoparasites and other material from the bodies of other fishes.

12. Fishes that prey mostly on sessile invertebrates, like sponges and coelenterates, are highly evolved diurnal species, including certain chaetodontids, pomacentrids, balistids, and monacanthids. These predators have specialized feeding structures and techniques that handle various noxious or toxic defensive features in their prey, including spines, spicules, nematocysts, tough fibrous tissues, and heavy armour. And they take these sessile animals in daylight because only moving prey are effectively sensed by visually feeding predators after dark.

13. Characteristics developed in feeding on sessile benthic invertebrates have been modified in some fishes for grazing on benthic vegetation. Thus, many families, for example the Chaetodontidae, Pomacentridae, Balistidae, and Monacanthidae, include some strictly carnivorous forms that prey on benthic invertebrates, other forms that feed on both benthic invertebrates and vegetation, and still others, strictly herbivorous, that only graze on benthic vegetation.

14. On coral reefs there is no sharp distinction between fishes that feed on sessile invertebrates and those that graze on benthic vegetation: species in both categories tend to be colorful diurnal fishes with a small mouth that is part of a highly evolved digestive apparatus.

15. The plasticity in feeding habits and structures characteristic of higher teleosts that feed on benthic organisms has led to the multiplicity of closely related, and morphologically similar species that live together on coral reefs. This situation could not have evolved without effective barriers to interbreeding, which in turn requires that individuals recognize others of their own kind from among many very similar forms. This requirement has been met by having developed highly visible, species-specific color patterns. The distinctive nocturnal color patterns of some forms, for example *Zanclus* and certain chaetodontids, indicate that, although they are diurnal, certain of them need identifying features at night, as well as during the day.

16. The small mouth of higher teleosts is adaptive for feeding on the smaller plankters, like calanoid copepods, that compose the vast majority of organisms in the water column. This characteristic distinguishes diurnal planktivores, including certain pomacentrids, chaetodontids, and balistids, from the nocturnal planktivores, which include certain holocentrids and apogonids. Most nocturnal planktivores have the larger mouth of the generalized predators, and most of them feed primarily on the larger plankters, like crab megalops and mysids, that are most numerous in the water column over the reef at night.

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Sea Squirts

The Marine Iguana

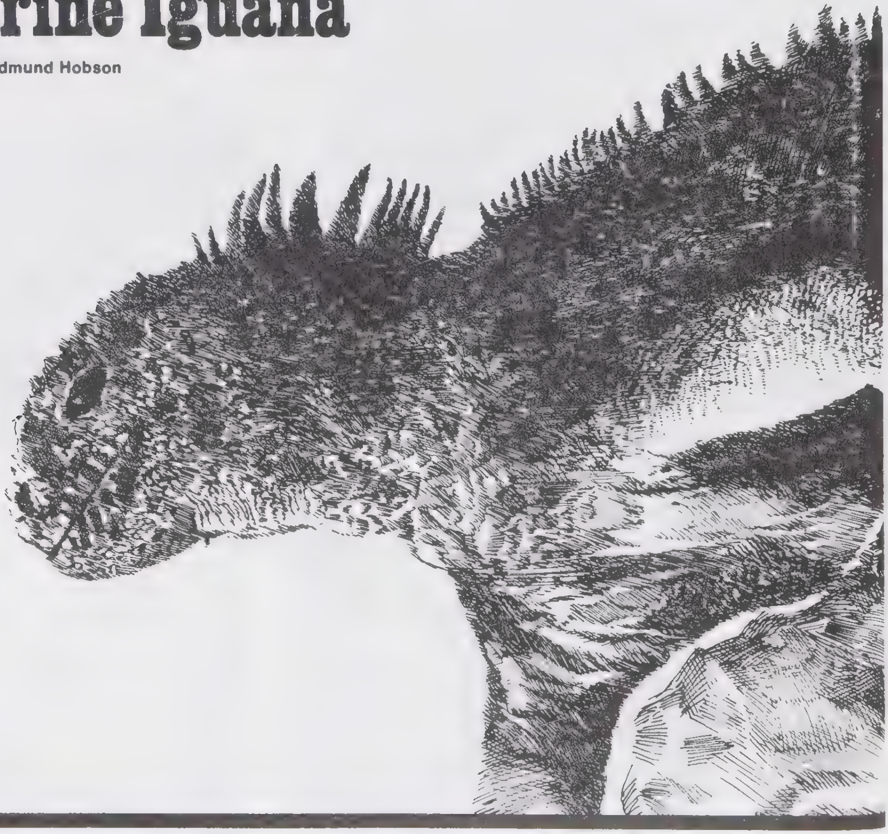
Text and photographs by Edmund Hobson

MARINE IGUANAS (*Amblyrhynchus cristatus*) are the only lizards on earth that feed in the sea. And the only land these creatures know are the barren shores of the Galápagos Islands, where they bask in the sun between feeding excursions into the surrounding waters.

These animals have captivated the imaginations of naturalists for centuries, but the writings they have generated often mix fact with fiction. Thus, when the English seaman James Colnett wrote in 1798 that marine iguanas "go to sea in herds afishing" he correctly described their swim from shore in groups, but incorrectly assumed they hunt fishes. The animals are herbivores that graze on seaweeds, a fact noted by Charles Darwin when in 1835 he visited the Galápagos Islands in H.M.S. *Beagle*.

Darwin wrote that marine iguanas swim "some hundred yards from shore," and dive for plants growing on the seabed. Other observers, however, have doubted they do this regularly. Almost 100 years after Darwin's account, William Beebe contended that marine iguanas grazed only on vegetation growing from rocks exposed at ebb tide. But Darwin was right. Marine iguanas are accomplished swimmers that move with undulations of body and tail, their legs trailing close alongside. Yet despite their submarine capability, these animals stay on the surface when moving to and from offshore feeding grounds. Perhaps they use terrestrial features to navigate, a possibility consistent with their way of swimming at the surface with head held high out of the water. Certainly iguanas see poorly underwater; this became apparent when, moving slowly, close to the bottom, I repeatedly approached to within a foot of submerged iguanas and found them seemingly unaware of my presence.

Iguanas arrive on the surface above their feeding ground, then dive to the sea floor. I have seen them grazing in 35 feet of water, and probably they seek food even deeper. The depths to which iguanas dive are not limited by how long they can stay underwater—Darwin long ago found them able to remain underwater more than an hour when necessary. Their submergence times relate to how deep the water is over the feeding ground. Thus, iguanas grazing near shore in water less than ten feet deep generally stay down less than five minutes, whereas those in deeper water often stay down fifteen minutes and longer. Considering their longer swim from shore, and their effort in getting from the surface down to the ocean floor, iguanas that feed in deeper water probably find it more efficient to stay longer on the bottom. Also, it is probably easier for them to remain on the bottom at greater depths. Iguanas are buoyant in shallow water, and bob to the surface as soon as they let go. Once free, they must swim vigorously to stay down. This difficulty is alleviated at greater depths because the increased water pressures compress their lungs, making them denser. At about 20 to 25 feet they show no noticeable tendency to rise or sink, but much below this they are denser than seawater and must actively swim to rise. Thus, an iguana I had chased to a depth of sixty feet appeared heavy in the water, and



swam with obvious effort when it headed toward the surface. It seems likely that iguanas can regulate their relative density somewhat by varying the amount of air in their lungs. If so, they would carry more air on deeper dives, and this would let them stay longer at greater depths.

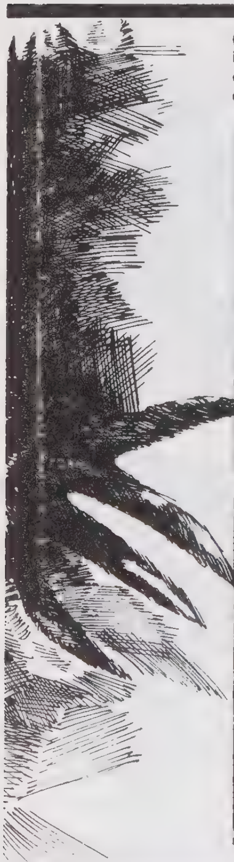
Even though foraging iguanas may range far afield, and dive to the bottom in relatively deep water, much of their grazing occurs at the edge of the sea. Here their hook-like claws cling securely to rocks exposed with a falling tide, and though often they are periodically submerged under the thunderous crush of breaking waves, the surging tons of white water fail to dislodge them.

When marine iguanas enter the sea to forage, their body temperature drops to that of the surrounding water. And in those parts of the Galápagos Islands where iguanas are most numerous, sea temperatures often hover around 70° F, which is cold for equatorial waters. Thus these unique creatures are most active at their lowest temperatures—a striking exception to the valid generalization that reptiles are most active at their higher temperatures, and here a vital adaptation.

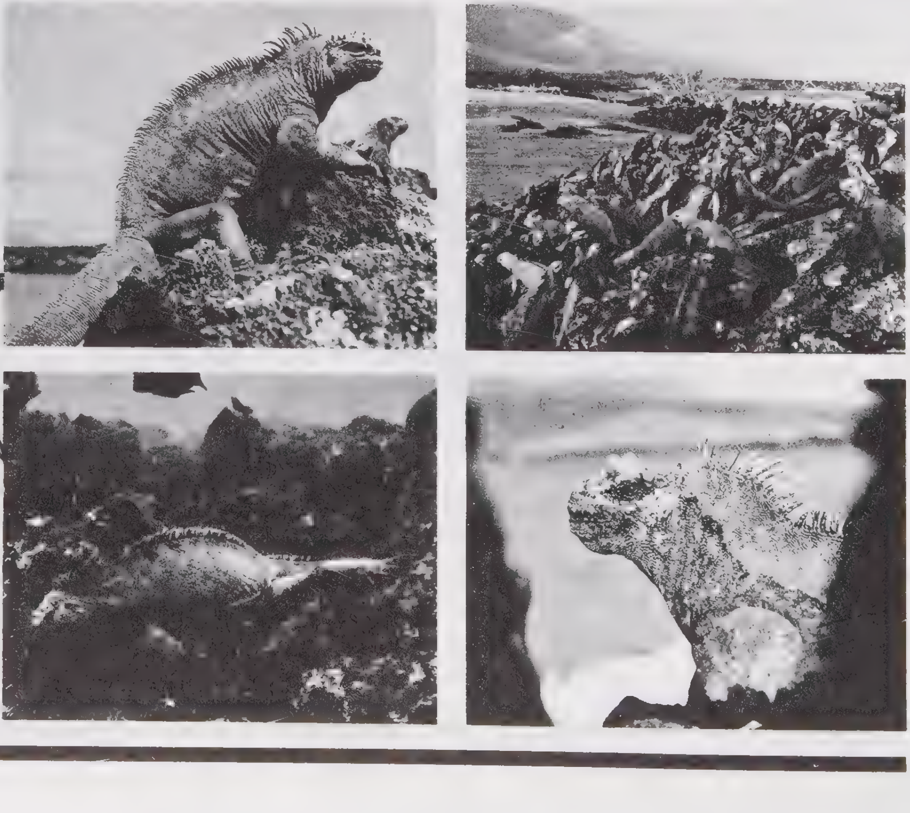
Marine iguanas basking on rocks ashore during the day are warmed by the equatorial sun. George Bartholomew of the University of California found that basking iguanas actively maintain their body temperatures within narrow limits —95 to 98° F—by changing position, and thus their angle of exposure to the sun. This throws new light on one of Darwin's better-known observations. Darwin noted that basking iguanas refuse to be driven into the sea, and when he hurled one into the water it immediately returned to shore. These animals want to stay out of the water, Darwin reasoned, because they fear sharks. Other observers over the years have duplicated Darwin's experience, and have accepted his reasoning. But Bartholomew's work suggests a more plausible explanation: having attained body temperatures up to 28° F above that of the sea, iguanas basking in the sun are simply reluctant to cool off suddenly, and will enter the water only to feed. Iguanas that have not warmed up fail to show this aversion to getting wet. Thus, when iguanas have just returned to shore from feeding, and their body temperatures are still that of the sea, they will reenter the water without hesitation when approached by a human being.

Iguanas do not suffer the threat from sharks that Darwin imagined. Certainly it is unreasonable to suggest that iguanas avoid the sea through "fear." They might seem especially vulnerable when swimming at the surface, especially with their heads out of the water. But though occasionally sharks take iguanas as prey—some have been found in shark stomachs —there is no good reason to assume that sharks threaten iguanas more than they threaten other marine animals. I have seen several sharks (gray sharks, white-tipped sharks, and hammerheads) pass close below iguanas swimming on the surface, and they gave no sign of regarding these lizards as prey.

Marine iguanas still fascinate visitors to the Galápagos Islands, and science is continually assessing new information about them. But we remain far from fully understanding the unusual biology of these extraordinary animals.



(Above, left) Marine iguanas ashore on Fernandina; (right) a large assemblage of the reptiles basking in the sun on this Galápagos island. (Below, left) Marine iguana grazing on the sea floor in fifteen feet of water off Fernandina; (right) marine iguana on Española (Hood), showing the multi-color patterning that distinguishes the iguana of that island from the plain gray forms occurring elsewhere in the Galápagos.



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Doppler structure in echoes from schools of pelagic fish

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The frequency distribution of energy in direct path echoes from three schools of pelagic fish is presented. One-half-second 30-kHz CW pulses were used to study motions internal to the fish schools from distances up to 1200 m. The measured Doppler spread of echo energy ranged from 30 Hz to 70 Hz. The Doppler spread-at-side aspect is related to swimming motions by a simple algebraic model based on Bainbridge's equation relating fish swimming speed, length, tail-beat amplitude, and tail-beat frequency. The mathematical model was used to estimate the length of the fish in two of the schools. These length estimates agree with average fish lengths derived from school cruising speeds. Near head or tail aspect, the observed Doppler structure appears to be related to behavioral swimming characteristics.

Subject Classification: 80.45; 30.30, 30.80, 30.25.

INTRODUCTION

Based upon acoustic measurements, and visual observations, it is apparent that a school of fish is a dynamic system characterized by varying degrees of systematic as well as random motion. The scale of movements in a school ranges from rhythmical, swimming-associated body motions of individual fish, including tail movements, to erratic, rapid changes in speed, direction, and shape of the entire school. Between these extremes lie a variety of motions, including cruising, swimming bursts, short-term accelerations, the constant changing of relative positions of individuals in a school, and several behavioral characteristics.

Information on fish length, swimming endurance, and school dynamics are all contained in the motions associated with a school. Moreover, an appropriate tool exists for the study of school motions. It takes the form of a measurement of Doppler frequency shifts in acoustic echoes from a fish school. Although the measurement of Doppler structure has been frequently discussed, it has been infrequently attempted[1] and with even less frequent success.

The following material contains a description of the experimental method for measuring the Doppler structure in echoes from fish schools. The frequency spectra of narrow-band echoes from three pelagic fish schools are presented. Additional acoustically derived data on the three schools, an analysis of the data, and, where possible, relation of the acoustic data to biologically meaningful parameters are also presented. The three schools were studied in late July 1972 at the locations shown in Fig. 1.

I. EXPERIMENT

In the current application, the Doppler effect refers to the change in frequency (pitch) which occurs when sound waves are reflected from a moving object. A frequency shift is similarly observed when sound is projected from or received by a moving platform. The shift is toward higher frequencies if the relative motion of the receiver and reflector is closing, and down in frequency if opening. The amount of the frequency shift is proportional to the original frequency and to the relative speed of approach or regression of the receiver (projector) and reflector.

Conceptually, one needs to transmit a pulse sufficiently narrow in bandwidth to resolve the degree of motion expected and then determine the distribution of energy in the echo as a function of frequency. The distribution of echo energy can then be related to a distribution of motions (velocities along the direction of propagation of sound) in the school of fish.

Though simple in concept, the execution of an experiment designed to make quantitative measurements of the Doppler structure in echoes from fish schools is sufficiently complex to make a computer-controlled data acquisition system desirable, if not a necessity.

The data acquisition system illustrated in Fig. 2 was designed around a 12-bit minicomputer with a memory cycle time of 1.6 μsec and 8192 words of core storage. The system was interfaced to an existing hull-mounted 30-kHz sonar on the NOAA Research Vessel *DAVID STARR JORDAN.* The *JORDAN*'s 11-kHz sonar was used to collect ancillary data on the track of the fish school. The vertical and azimuthal beam widths of each sonar were approximately 12° at the -3-dB points. Both sonars could be trained through 360° in azimuth and the 30-kHz transducer was vertically steerable. The 11-kHz source level was 220 dB while the 30-kHz source level was 224 dB, both relative to 1 μPa at 1 m. A high-level interpretive software system, originally supplied by the computer manufacturer, was substantially modified and expanded to be used in controlling the experiment. This approach allowed both rapid, algebraic-like interaction with the data acquisition process (e.g., updating range, speed of sound, etc.), as well as *in situ* modifications of the experimental method, which would not have been practical if the software had been coded directly in machine language.

In a typical sequence, a fish school was detected with the 11-kHz sonar at a range of 300 to 700 m from the ship. The ship was stopped and allowed to drift with wind and current. There were two reasons for stopping the ship. The first was a desire to study single fish schools for extended periods, for example, an hour or more. Contact with a fish school from a ship moving at

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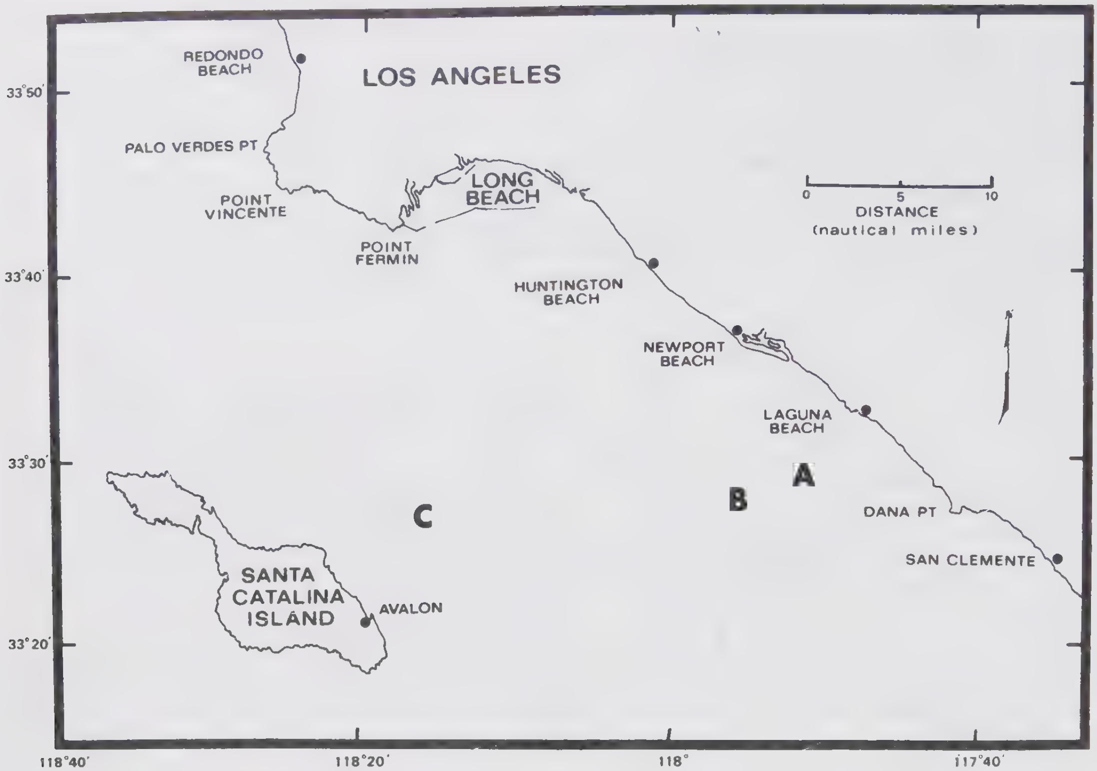


FIG. 1. Location of schools studied in July 1972.

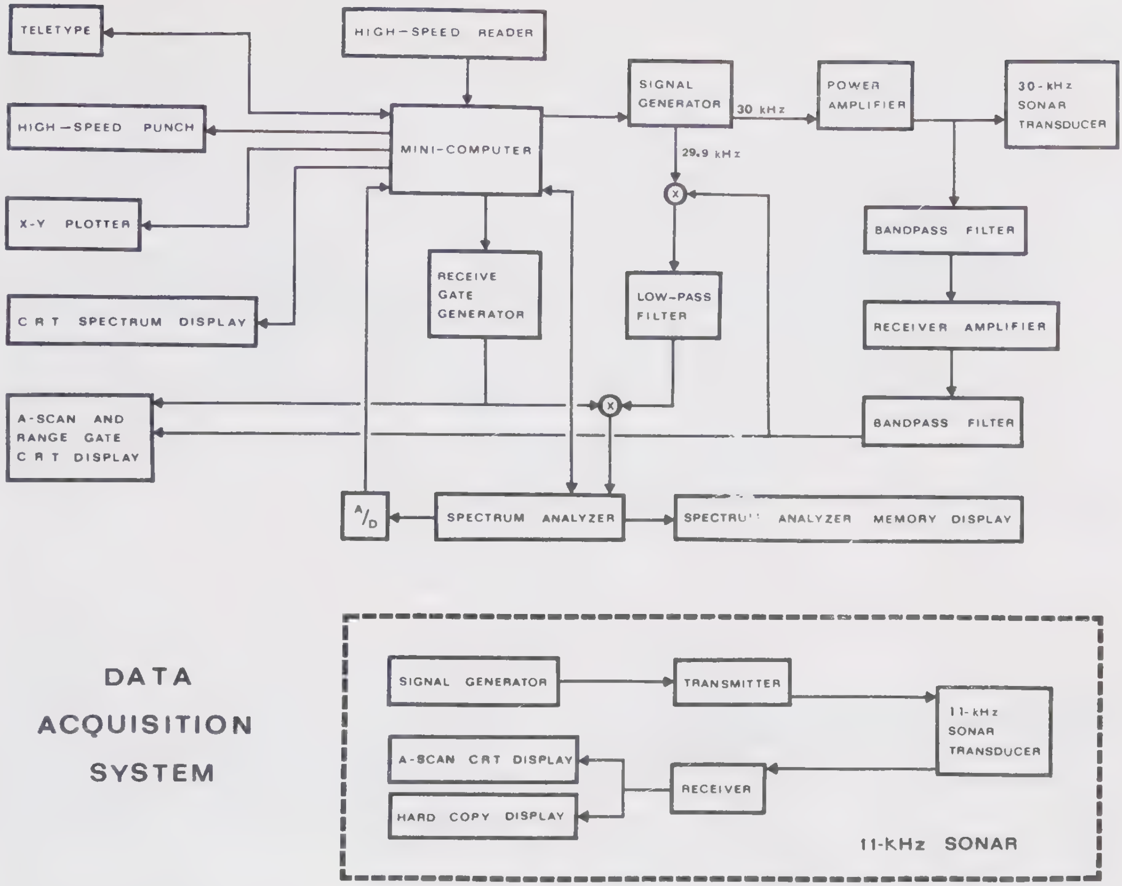
6 to 12 knots along a straight track lasts no more than a few minutes. The second reason for allowing the ship to drift was related to equipment limitations. The 30-kHz sonar was originally designed to transmit pulses of up to 80-msec duration. It was necessary to slow the pulse repetition rate to one pulse each 100 sec in order to use the $\frac{1}{2}$- and 1-sec pulses required for measuring Doppler structure. At faster pulse repetition rates, noticeable degradation of the 30-kHz sonar source level was apparent. The 100-sec interval dictated that the ship–fish geometry change as slowly as possible in order that necessary ensemble averaging could be performed without catastrophic violations of the requirement of stationarity.[2] Drifting, as opposed to low-speed maneuvering, was determined to be the practical solution to this problem.

The drift rate and direction, with respect to the water column at the fish range and depth, were accurately determined on a periodic basis by measuring the direction and amount of the maximum Doppler shift of volume reverberation. The primary contributor to volume reverberation is plankton which drifts with the body of water. Thus, an accurate measure of the ship's motion relative to the water column is readily available. This is essential if accurate measurements of fish school track and swimming speed are to be made. The presence of a stable reference, such as the frequency of the volume reverberation, also allows a first-order compensation for the effects of making Doppler structure measurements from a moving platform rather than a stationary one.

Tracking of the target was started with the 11-kHz sonar, aided by a programmable calculator, as soon as the ship stopped. When a steady drift rate and direction were established, the computer was instructed to generate and transmit, via the 30-kHz sonar, a pulse of $\frac{1}{4}$-, $\frac{1}{2}$-, $\frac{3}{4}$-, or 1-sec duration, depending on the target range. The data presented later in this paper are from the $\frac{1}{2}$-sec transmissions.

At the end of the 30-kHz transmission, the signal generator frequency was switched to 29.9 kHz. This signal was then used to heterodyne the received signal, spread about 30 kHz by the Doppler effect, to a band between 0 and 200 Hz. The sum band was rejected by a low-pass filter. At a time determined by the computer from the target range and average speed of sound over the ray path to the school, a command was issued to generate a range gate in the form of one-half of one cycle of a cosine function. This form of range gate was combined with similar temporal weighting in the spectrum analyzer to suppress side lobes in the frequency domain.

Again, under computer control, a command was issued to capture the fish school echo in a spectrum analyzer memory. The memory was automatically displayed on a CRT. Immediately after the echo was captured, its


TELETYPE
HIGH-SPEED READER
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MINI-COMPUTER
X-Y PLOTTER
CRT SPECTRUM DISPLAY
A-SCAN AND RANGE GATE CRT DISPLAY
RECEIVE GATE GENERATOR
SIGNAL GENERATOR
30 kHz
29.9 kHz
POWER AMPLIFIER
30-kHz SONAR TRANSDUCER
LOW-PASS FILTER
BANDPASS FILTER
RECEIVER AMPLIFIER
BANDPASS FILTER
A/D
SPECTRUM ANALYZER
SPECTRUM ANALYZER MEMORY DISPLAY
DATA ACQUISITION SYSTEM
SIGNAL GENERATOR
TRANSMITTER
11-kHz SONAR TRANSDUCER
A-SCAN CRT DISPLAY
HARD COPY DISPLAY
RECEIVER
11-kHz SONAR

FIG. 2. Data acquisition system for the measurement of fish-school Doppler structure.

spectrum was digitized and transferred from the spectrum analyzer to the computer for display on a second CRT, and for output to punched paper tape for later analysis. An option to accumulate and display an ensemble average was available but was infrequently used due to the length of time for on-line computer corrections for the effects of the ship's motions.

All displays were made available for examination until the 100-sec-waiting interval had elapsed. At the end of that time, the spectrum analyzer was released to accept new data and the sequence repeated. The sequence was occasionally interrupted for a period of less than 10 sec for an update on school range.

During the 100-sec delay between 30-kHz pings, the 11-kHz sonar was used to obtain bearing and range information. A minimum of 10 pings at 2-sec intervals was used to determine the direction and range of the school on the basis of maximum acoustic return. The 11-kHz sonar was not operated simultaneously with the 30-kHz sonar because of a problem of mutual interference.

II. DATA

A. Data format

The echo from a fish school is stochastic. Consequently, the Fourier transform of a single echo is likewise stochastic. In order to obtain a physically more meaningful representation of the frequency distribution of energy scattered from a school, the energy spectral density was computed by performing an ensemble average over several sequential echoes. The indicated calculation was performed as a running average over seven successive pings throughout the available data sequence for each of three schools.

Aspect and school swimming speed relative to the water column are included in the caption for each figure displaying a sequence of energy spectra as a function of Doppler frequency shift. A more detailed description of aspect and speed are contained in the discussion of each set of spectra. Aspect and swimming speed numbers associated with a particular energy spectrum are averages taken over the same time interval as the ensemble average used to compute the spectrum. An unshifted

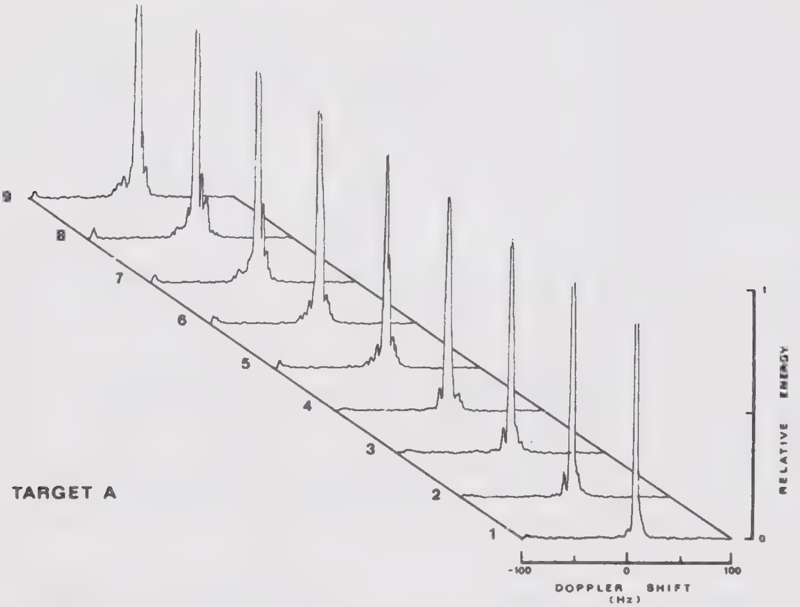

FIG. 3. Energy spectra of side aspect echoes from Target A, spectra 1–9. Pulse length: 0.5 sec. Center frequency: 30 kHz. Average swimming speed: 0.85 m/sec.

echo at the 30-kHz carrier frequency would appear at a 0-Hz Doppler shift. A pulse length of $\frac{1}{2}$ sec indicates a frequency resolution of 2 Hz. The energy spectral density was computed at 1-Hz increments for all of the data presented.

If any attempt is to be made to interpret, explain, or relate the Doppler structure of an echo to the motions in a fish school, supporting data on school track, mean school speed, and the aspect angle between the school track and the sonar are minimum requirements. Further, track and swimming speed data can be of value in the study of fish schools in a primary role, e.g., in behavior and energetics studies. Consequently, a substantial effort was directed towards obtaining accurate fish and ship's track information, concurrent with the Doppler structure measurements.

B. Target A

Target A was detected at approximately 9 a.m. on 21 July 1972 in about 325 fathoms water depth, approximately 4 miles southwest of Laguna Beach, California. The target dimension along the direction of the sonar beam varied from 60 to 120 m during the period of observation. Measurements of target sizes were made with 1-msec, 11-kHz pulses.

Figure 3 illustrates a sequence of nine energy spectral density curves for echoes from Target A. Each curve represents a running average over seven echoes. During the time of acquisition of the data shown in Fig. 3, the sonar beam was, on the average, nearly orthogonal to the swimming direction of the fish school. The average swimming speed during this interval was 0.85 m/sec.

An intense narrow return near zero Doppler shift is apparent in all spectra presented. This return is due to volume reverberation. Each spectrum has been shifted in frequency before averaging, to align the volume reverberation in frequency and to place the reverberation frequency at the mean frequency of the volume return in the set averaged. This process was used as a first-order correction for the Doppler effects due to the ship's oscillatory motions, principally roll.

Since the sonar beam and the direction of school travel were approximately orthogonal, the echo from the fish school appears symmetrically distributed about the volume reverberation return. The frequency of the volume reverberation is a convenient reference of no motion, relative to the water column. The echo in the spectrum numbered 1 is present but very weak. Therefore, the spread of energy at the base of the volume reverberation return in spectrum 1 can be used to indicate the small contribution of side lobes (due to the finite pulse length) to the spectral level in the vicinity of the volume reverberation return.

A close examination of spectra numbers 5–9 in Fig. 3 will reveal a return with a Doppler shift of about −100 Hz. This return is due to bottom reverberation. As a sequence of echoes was obtained from a school, both water depth and the range to the target varied. Therefore, for some combinations of water depth and range gate settings, reverberation from the bottom appears at a frequency determined by the ship's drift (wind) with respect to the water and the movement of the water column with respect to the bottom (currents).

A sequence of near-tail aspect echoes from Target A is presented in Fig. 4. The aspect varied in a linear manner from 30° (near-tail aspect) at spectrum 21, to about 5° from tail aspect at spectrum 29. The school

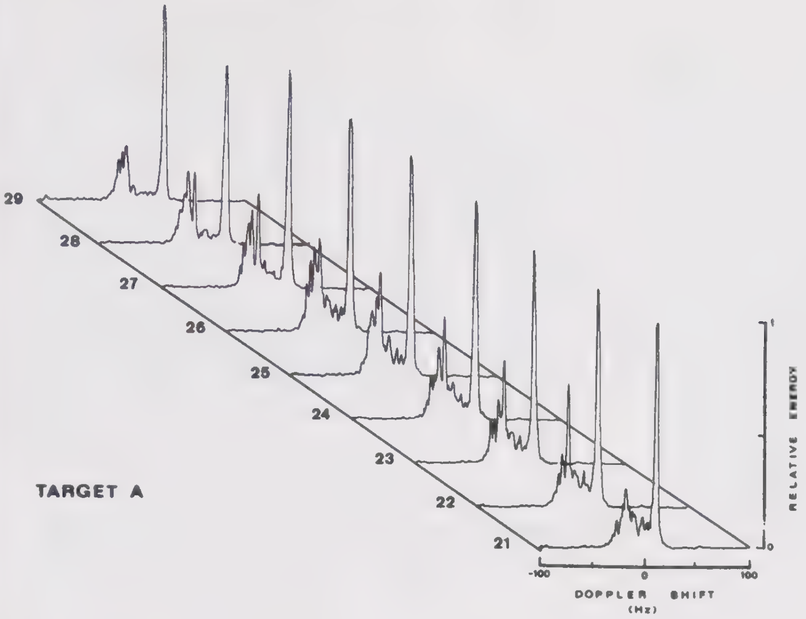

FIG. 4. Energy spectra of tail aspect echoes from Target A, spectra 21–29. Pulse length: 0.5 sec. Center frequency: 30 kHz. Average swimming speed: 0.05 m/sec.

swimming speed was almost constant at an average 1.05 m/sec during the interval between spectra 21 and 29.

The echo is seen in Fig. 4 as a distribution of energy centered about a negative Doppler shift which varies from about 35 Hz at spectrum 21, to 40 Hz at spectrum 29. The changing Doppler shift of the echo is principally due to the change in the sonar beam axis with respect to the school travel direction.

C. Target B

This 40-m-wide target was located at approximately 11 a.m. on the north flank of the Lasuen Seamount. The target was at a depth of approximately 40 m. The water depth was 250 fathoms.

A sequence of energy spectra from Target B is shown in Fig. 5. During the interval for which the spectra are

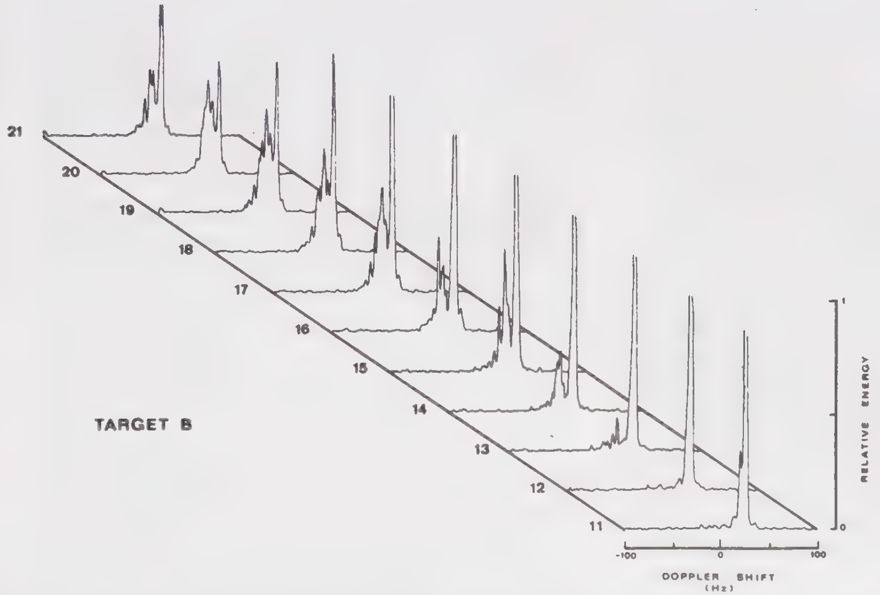

FIG. 5. Linear representation of the energy spectra of echoes from Target B, spectra 11–21. Pulse length: 0.5 sec. Center frequency: 30 kHz. Aspect was near 45° from tail aspect. Swimming speed varied from 1.4 m/sec at spectrum 11 to 0.5 m/sec at spectrum 21.

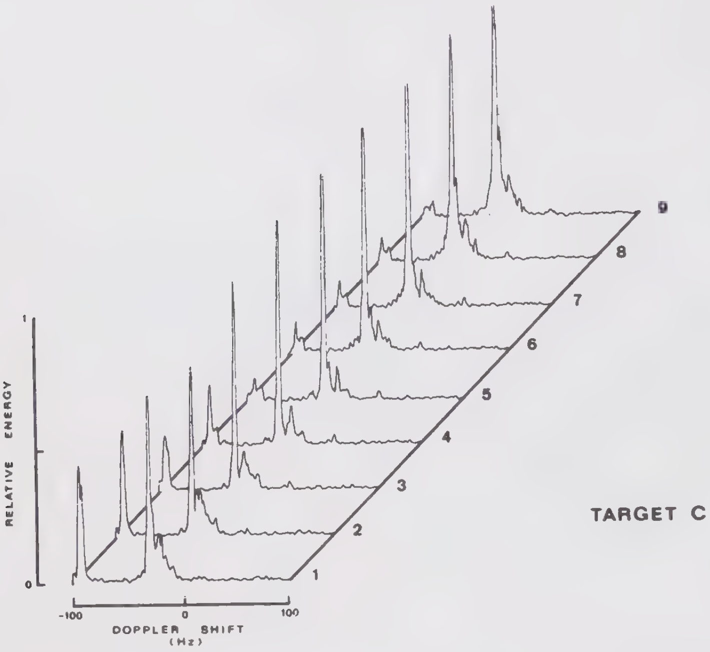

FIG. 6. Energy spectra of head aspect echoes from Target C, spectra 1–9. Pulse length: 0.5 sec. Center frequency: 30 kHz. Swimming speed: 0.45 m/sec.

provided, the school aspect varied less than 5° from a tail-quarter aspect. At the time of spectrum 11, the aspect was 40°. The aspect increased linearly to 50° at the time of the center echo in the ensemble average which resulted in spectrum 16, and remained at 50° until the end of the data sequence. The school swimming speed remained near 1.4 m/sec between spectra 11 and 16. A decrease in swimming speed to 0.5 m/sec occurred between spectra 16 and 19. The speed remained constant at 0.5 m/sec from spectrum 19 to the end of the data sequence.

The echo from the fish school can be seen in Fig. 5 as a distribution of energy centered about a lower frequency than the water column reference, the volume reverberation return. The volume reverberation appears at a positive Doppler shift due to the ship's drifting speed and the relative angles between the direction of drift and the sonar beam axis. The frequency separation between the volume reverberation and the center of the fish echo energy distribution can be used to measure the component of fish school speed along the sonar beam axis. Calculations of school swimming speed from the component of motion along the sonar beam and the track-derived angle between the sonar beam and the swimming direction of the school exhibit the expected agreement in speed based on school track data alone.

The increase in echo level between spectra 11 and 15 was associated with an apparent compaction of the school and with the observed change in swimming direction. The increase in echo level is also consistent with the change in aspect angle from near 40° to 50°, i.e., 10° nearer side aspect.

D. Target C

Target C was located at approximately 1 p.m. on the same day in the San Pedro Basin near Santa Catalina Island. The water depth was about 475 fathoms. The target size remained approximately 60 m throughout the period of observation. This fish school was also estimated to be near a depth of 40 m. This estimate, as well as those for the two previous schools, was derived by comparison of the target acquisition range with the acoustic propagation path. The propagation path was computed at sea from temperature profiles of the water column taken near the school locations during the same period.

Both aspect and swimming speed remained nearly constant during the interval covered by the data in Fig. 6. The fish were swimming almost directly at the ship during the entire period of observation. The ship, however, was drifting away from the fish at a greater rate than the fish swimming speed. Consequently, although both volume reverberation and the echo from the school are shifted down in frequency, the distribution of echo energy appears at a higher frequency than the water motion reference, volume reverberation. The difference of about +20 Hz between the volume reverberation return frequency and the echo frequency is consistent with the track derived swimming speed of 0.45 m/sec.

The return near–100-Hz Doppler shift is bottom reverberation. As the period of observation progressed, the ship drifted into slightly deeper water and the amount of bottom reverberation coincident with the echo was reduced.

III. ANALYSIS AND INTERPRETATION

A. Fish size and cruising speed

Each of the schools for which Doppler spectra are presented was observed for about one hour. A detailed analysis of the swimming speed reveals periods of relatively constant swimming speeds. An average length can be computed for the fish in each school if one assumes that the observed constant swimming speeds correspond to cruising or sustained swimming speeds described by Bainbridge[3] and by Mangan.[4] Measured sustained speeds for fish generally range between 2 and 4 body lengths/sec. The best available estimate of the low cruising speed of marine species appears to be the work of Mangan in 1930. The average cruising speed for 17 marine species common to the North Atlantic was 3.2 body lengths/sec.

Based on cruising speeds of 0.9, 0.85, and 0.45 m/sec for Targets A, B, and C, respectively, one can calculate the length of an average fish in each school. The lengths which result from this calculation are 0.29 m for Target A, 0.27 m for Target B, and 0.14 m for Target C.

B. Fish size and Doppler structure

A detailed examination of fish school tracks and swimming speed records indicate that rapid accelerations and decelerations within a fish school, and accompanying changes in school shape due to a lag in response between the fish in the front of the school and those in the back may be common. Under these conditions, one would expect a relatively wide distribution of swimming speeds at a particular instant during a transient in the school's speed of advance. In order to reduce the impact of these behavioral movements on the estimate of fish size from body and tail motions, we have restricted our size calculations to cases in which the fish presented a side aspect to the sonar beam. In this manner, the Doppler spread due to a distribution of swimming speeds along the direction of school advance was minimized, and the effect of body motions perpendicular to the direction of school headway was enhanced.

In a study of three species of fish, Bainbridge[5] determined that the swimming speed (V) of all three species could be calculated from their total length (L) and their tail-beat frequency (F) by the relation of Eq. 1.

$$V=(L/4)(3F-4). \tag{1}$$

The swimming speed may be expressed in meters/sec if length is in meters and tail-beat frequency is in hertz. Since the dominant schooling species of fish in the Los Angeles Bight are carangiform swimmers, we assume this mode of swimming. Although the entire body of carangiform swimmers takes part in the swimming motion, the maximum excursion occurs between the tip of the caudal fin and the base of the tail. Assuming that any deviations from sinusoidal motion of the tail are of second order, one may write an expression for the maximum speed ($\widehat{v_t}$) of the fish's tail in a direction perpendicular to the direction of swimming. Thus $\widehat{v_t}$ is given by

$$\widehat{v_t}=2\pi FA, \tag{2}$$

where A is the single-sided amplitude of the tail excursion. Working with Bainbridge's data,[6] we find that the average tail-beat peak-to-peak excursion can be expressed as 0.183 times the fish length for all species studied. Consequently, Eq. 2 can be rewritten as

$$\widehat{v_t}=0.183\pi FL. \tag{3}$$

The Doppler frequency shift expected from a sound scatterer with a speed given by Eq. 3 can be written as

$$\widehat{\Delta f}=f_0(2\widehat{v_t}/c). \tag{4}$$

The maximum frequency shift $\widehat{\Delta f}$ is expressed in hertz, the term f_0 is the unshifted sonar transmission frequency, and c is the speed of sound in meters/sec.

Combining Eqs. 1, 3, and 4 results in an expression given in Eq. 5, for the length of the fish in terms of its swimming speed and the maximum observed Doppler shift when the fish presents a side aspect to the sonar beam.

$$L=0.65\,c\widehat{\Delta f}/f_0-V. \tag{5}$$

The numerical coefficients of $c\widehat{\Delta f}/f_0$ and V both have units of time. Thus L is expressed in meters. In the discussion which follows, the appropriate values of c and f_0 are 1520 m/sec and 30 000 Hz, respectively. Substitution of these values into Eq. 5 results in

$$L=3.3\times10^{-2}\,\widehat{\Delta f}-V. \tag{6}$$

C. Target A

The energy spectrum shown in Fig. 7 is the result of averaging the spectra of three echoes from the data obtained for Target A. The relative positions of the fish school and of the ship at the times of the three echoes indicate a near-broadside aspect on the fish school at the time of each ping.

The dominant return in Fig. 7 is volume reverberation. Since, at side aspect, there is no mean headway component along the sonar beam axis, the echo from the fish

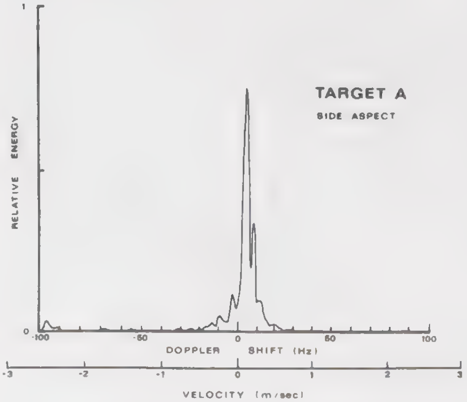

FIG. 7. Average energy spectrum for three side aspect echoes from Target A. Pulse length: 0.5 sec. Center frequency: 30 kHz.

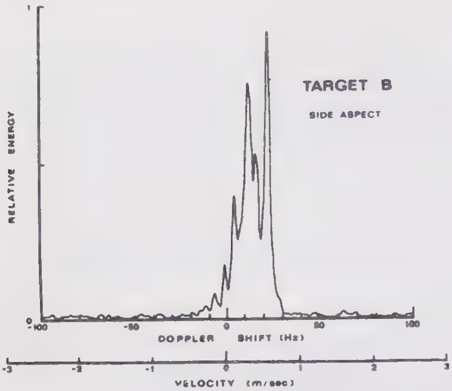

FIG. 8. Average energy spectrum for three near-side aspect echoes from Target B. Pulse length: 0.5 sec. Center frequency 30 kHz.

is centered about the same frequency as the volume reverberation and appears in Fig. 7 as a low-level spread of energy about the principal reverberation peak. A comparison of spectrum number 1 in Fig. 3, in which a very low-level target is present, and spectrum number 8 in the same figure, which contains a target of essentially the same strength as in Fig. 7, is of value in determining that the contributions of side lobes of the reverberation peak to frequencies removed by more than 10 Hz from the reverberation center frequency to the fish echo are negligible. Thus, the observed spread of 50 Hz about the reverberation peak can be attributed to motion internal to the fish school. At the mean rate of advance of the school during this period under consideration (0.53 m/sec), even the most extreme deviation (90°) of individual fish headings from the mean school heading could not have accounted for the observed frequency spread. Assuming that the observed Doppler structure was due principally to body and tail swimming motions and that the maximum observed frequency shift was due to peak tail velocity, one can calculate a fish length of 30 cm. This is in good agreement with the estimate of a 29-cm length derived from the school cruising speed.

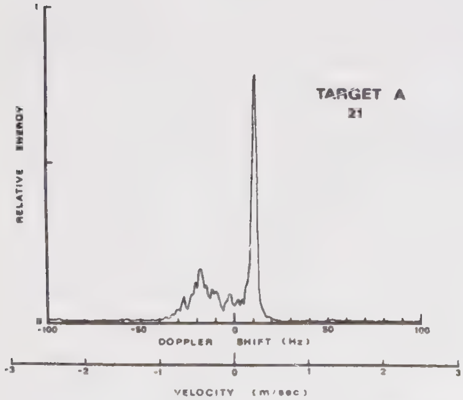

FIG. 9. Energy spectrum for seven tail aspect echoes from Target A, centered on ping 21. Pulse length: 0.5 sec. Center frequency: 30 kHz.

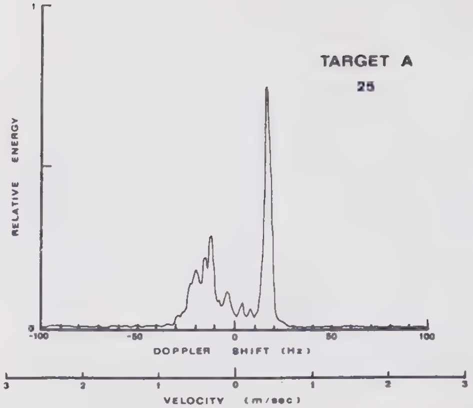

FIG. 10. Energy spectrum for seven tail aspect echoes from Target A, centered on ping 25. Pulse length: 0.5 sec. Center frequency: 30 kHz.

D. Target B

The averaged spectra for three echoes from Target B are presented in Fig. 8. The sonar beam intercepted the fish school track at an 18° (±2°) deviation from broadside during the three-ping sequence. This results in a 0.25-m/sec component of headway away from the ship. The average swimming speed of the fish during the sequence was 0.84 m/sec. The largest return in Fig. 8 is volume reverberation. The echo from the fish school is Doppler shifted to a center frequency which is 10 Hz lower than the volume reverberation. The magnitude and direction of the shift are in excellent agreement with the values expected on the basis of the track data. The echo is symmetrically distributed around its peak with a maximum spread of 70 Hz. Substitution of these data into Eq. 6 yields a calculated average fish length of 27 cm. This length is the same as that calculated from school cruising speed.

E. Interpretation of tail aspect Doppler structure

As the target aspect varies from side to head or tail, the Doppler structure rapidly becomes less sensitive to tail and body swimming motions and more sensitive to internal school dynamics. Short-term accelerations associated with individual tail beats, short bursts and periods of slightly slower swimming due to the constantly changing relative positions of fish within a school, and components of tail motion in the forward or aft direction are all short-term motions which can affect the frequency distribution of an echo from a fish school.

While all of the short-term effects mentioned undoubtedly contribute to the Doppler spread at tail aspect, the observed Doppler spread appears to be most readily interpreted in terms of long-term distributions in swimming speeds within a school and changes in those distributions. Three examples of Doppler structure will be cited to illustrate the basis for this hypothesis.

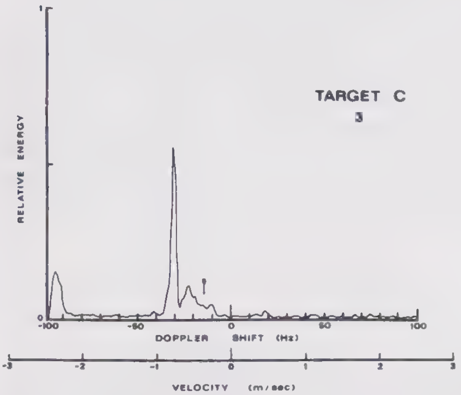

FIG. 11. Energy spectrum for seven head aspect echoes from target C, centered on ping 3. Pulse length: 0.5 sec. Center frequency: 30 kHz.

Figures 9 and 10 are averages of seven spectra each from the Target A echoes. Both spectra are taken from a position in the Target A sequence in which the fish presented close to a tail aspect to the sonar beam. A close examination of either spectrum reveals a distribution of echo energy with frequency around the echo peak at about –15 Hz. The distribution appears skewed toward Doppler shifts smaller than the shift of the echo peak. This distribution in frequency corresponds to a similar distribution in motion along the swimming direction of the school. The maximum swimming speed, derived from Fig. 10, is 1.2 m/sec. The minimum speed observed can be estimated as less than 0.3 m/sec, even though the lower limit is masked by volume reverberation. The average swimming speed of the school corresponding to the spectrum in Fig. 10 was 1.1 m/sec.

The skew towards low-speed swimmers persisted over a long interval (see Fig. 4) and is consistent with the hypothesis of an elongation in the fore and aft school dimension during this period, based on the echo level and an 11-kHz sonar measurement of the school dimension along the direction of school travel. A simple calculation based on the differential swimming speed and the duration of the observed skew in speeds indicates that the school elongation during this period of relatively constant cruising was due to some behavioral characteristic shared by all of the school members rather than differences in swimming capabilities or preferences associated with individual fish. If the slow swimmers at echo 21 had maintained that speed through echo 26, and likewise, if the high-speed swimmers had maintained their speed, the school dimension along the direction of travel would have been elongated by more than six times that observed.

A reduction of 40% in the dimension of the school along its direction of travel occurred between pings 26 and 27. An increase in echo level accompanied the apparent compaction. This change in the school was accompanied by a noticeable reduction in the skew of the echo toward low-speed scatterers. These observations would indicate a change in swimming behavior in which the compaction of the school was achieved by the slower-swimming fish increasing their speed rather than the faster fish in the leading edge slowing down. The narrowing of the distribution of swimming speeds was followed approximately 6 min later by a high-speed swimming burst.

The third illustration of the impact of swimming behavior on tail or head aspect Doppler structure is taken from the sequence of echoes obtained from Target C. Spectrum No. 3 from the sequence illustrated in Fig. 6 is enlarged and presented in Fig. 11. This spectrum is typical of the 45-min-long head aspect data set. The peak near –90° Hz is bottom reverberation. The largest peak is volume reverberation. The arrow indicates the projected target Doppler shift, based on the school mean swimming speed of 0.45 m/sec. The minimum swimming speed is approximately 0.1 m/sec while the maximum is almost six times greater at 0.58 m/sec. This distribution exhibits a pronounced peak about a frequency shift corresponding to 0.17-m/sec swimming speed. Since the pattern persisted throughout a 45-min period, and since the school dimension did not vary substantially during this period, the observed distributions and their extremes are taken as evidence of a behavioral pattern of swimming. Although there is little direct, documented evidence of such behavior in the open ocean, the sustained pattern of the Doppler structure in echoes from Target C is qualitatively consistent with the accelerations and subsequent gliding associated with filter feeding observed in several species of pelagic fish under laboratory conditions. These species include jack mackeral and anchovy, both of which are common in the Los Angeles Bight.

IV. SUMMARY AND CONCLUSIONS

The internal dynamics of three schools of pelagic fish was investigated, with 1/2-sec acoustic pulses from a 30-kHz sonar. Echoes resulting from these transmissions were analyzed to determine the frequency distribution of echo energy. The observed frequency distributions were interpreted as the result of Doppler shifts due to motion in the fish school. Observed Doppler structure was divided into that caused by body and tail related swimming motions, near-side aspect, and to behavioral swimming characteristics, near-tail or -head aspect. Side aspect data were used to estimate fish length by use of a simple mathematical model. The estimates so derived were consistent with the estimates of fish length made on the basis of school swimming speeds. Tail and head aspect Doppler structure data were correlated with echo level, school dimensions, and school swimming speed to demonstrate that the observed Doppler structure could have resulted from special swimming behavior. In two cases the behavior changed the school dimensions, and in a third situation no change in school dimensions was observed.

The data and interpretations reported in this paper indicate two new applications of narrow-band, active sonar to the field of fisheries biology. Both involve the Doppler effect.

The first application is the accurate measurement of the direction and magnitude of maximum Doppler shift of volume reverberation relative to the sonar transmission frequency. This measurement allows an accurate estimate of the sonar platform motion relative to the water column. With this information in hand, a sonar with a high range resolution can be used to obtain an accurate track for a school of fish. This track and its first time derivative, the school swimming speed profile, both contain information of interest to the fisheries biologist, such as fish size and swimming endurance.

The second application of the Doppler effect is the direct measure of the spread of echo energy in frequency due to internal school dynamics. Information on swimming, schooling behavior, and fish size is contained in these data.

Either or both of the indicated applications of narrowband sonar may offer an independent check or viable alternatives to currently available methods of remote sensing of average individual fish sizes within a school.[7] It seems reasonable to caution the reader against weighting too heavily the excellent agreement between lengths derived from cruising speeds and similar estimates based on Doppler spread. While the agreement is encouraging, data are presented for only two schools. Further, the only true test of the acoustic technique will be in direct sampling.

The simple mathematical model presented in Sec. III relates maximum observed Doppler shift, school speed, and average fish length. A simple test of the sensitivity of the length estimate provided by this model indicates a strong dependence on the slope and intercept of Bainbridge's equation relating school swimming speed, fish length, and tail-beat frequency (Eq. 1). The length estimate is also quite sensitive to the coefficient which relates tail-beat amplitude and fish length during steady cruising. Equation 5 indicates a severe, but with care attainable, measurement accuracy requirement for the maximum Doppler spread and school speed.

The sensitivity of the model to its measured parameters can be viewed in two ways. First, a significant effort will be necessary in sea-going applications to insure that the required accuracy is achieved in the presence of sonar platform motions. An optimistic view, however, of the sensitivity of length estimates to Bainbridge's measured parameters is that the model may be sufficiently sensitive to allow resolution of species-specific differences, if they exist. In either case, while resource and time limitations precluded capture of the schools investigated and thus the direct validation of the acoustically derived length estimates, it is apparent from the data presented that such validation is now appropriate.

ACKNOWLEDGMENTS

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Special thanks are due Dr. V. C. Anderson of the Marine Physical Laboratory and to Dr. P. E. Smith of the Population Dynamics Group of the National Marine Fisheries Service, La Jolla, for their interest, support, and advice.

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Effect of Prey Distribution and Density on the Searching and Feeding Behaviour of Larval Anchovy *Engraulis mordax* Girard

J. R. Hunter and G. L. Thomas

INTRODUCTION

Laboratory estimates of the minimum concentration of food required for survival of marine fish larvae usually are much higher than the average concentrations of food in the sea (O'Connell and Raymond, 1970; Hunter, 1972). A common explanation for the fact that laboratory food requirements exceed natural food densities is that larvae are able to find and remain in patches of food in the sea which are considerably above the average food density estimated from plankton net catches. This explanation is supported in part by Ivlev (1961) who demonstrated with carp fry that an increase in the degree of aggregation of prey had the same effect on food consumed as an increase in the overall density of food material. A patchy distribution of larval food occurs under natural conditions. Thus, the effect of prey distribution on feeding behaviour of larval fish and the scale of "patchiness" of food items in the sea must be known to estimate the impact of food distribution on the feeding and searching behaviour of larval anchovy. This paper described some aspects of the effect of prey distribution and density on the feeding and searching behaviour of larval anchovy *Engraulis mordax* Girard.

The prey used in most of the experiments was the dinoflagellate, *Gymnodinium splendens*, which forms dense, stable, and easily-recognizable aggregations in rearing containers. *Gymnodinium* is readily cultured (Thomas et al., 1973), and promotes growth in larval anchovy equivalent to a wild plankton diet during the first week in the life of an anchovy larvae (Lasker et al., 1970). For comparative purposes we also used the rotifer, *Brachionus plicatilis.*

Larvae were reared from the egg in air conditioned rooms in static sea water which varied in temperature from 17° to 19°C. Anchovy eggs hatch in about 2 days when kept at these temperatures. At hatching the yolk-sac larvae have functional olfactory organs and naked neuromasts but they do not have a functional eye (O'Connell, pers. comm.). About 50 h after hatching the mouth is functional, the gut expanded, and occasionally food is present in the gut (D. Kramer, unpubl.), although we have never seen larvae actively feeding at this stage. About 72 h after hatching only a few granules of yolk remain (D. Kramer, unpubl.), the eye becomes functional and active feeding begins.

During the first few days after yolk absorption anchovy larvae have a higher food density requirement than at any other time in the larval stage (Hunter, 1972). The larvae have a low level of feeding success, capturing only 11% of the prey at which they strike, and the volume of water searched for prey is much less than that for older larvae. In addition, at this stage, larvae die of starvation if they do not find food within 1.5 days (Lasker et al., 1970). These laboratory findings suggested that effect of food distribution was most important during the first days of feeding. For this reason we restricted our observations to larvae of ages 1 to 8 days.

METHODS OF FORMING PATCHES OF *GYMNODINIUM*

We consider here our observations of the behaviour of *Gymnodinium* aggregations and our techniques for formation of the aggregations. These observations are important because the aggregations played a critical role in our experiments; if similar aggregations form under natural conditions, they could be an important factor in the survival of marine fish larvae. *Gymnodinium splendens* is an unarmored, marine, halophytic dinoflagellate about 53 μ in diameter. Reproduction appears to be sexual and occurs under natural conditions only at night (Sweeney, 1959).

In the laboratory distinct, visible aggregations or patches of *Gymnodinium* were produced under a variety of conditions. The patches were yellow-green, and occurred at the surface in daylight and in darkness. The aggregations had a dense central mass with striae of cells extending from it. Cells were most dense at the water surface; the average density for 8 aggregations measured at the water surface was 30,000 cells/ml, whereas 10 cm below the water surface the mean density was 250 cells/ml. The patches varied in diameter from a few mm to ones greater than 10 cm. Occasionally more than one patch formed in a larval-rearing container.

Our procedure for establishing an aggregation of *Gymnodinium* in a rearing container was simply to add an inoculum sufficient to bring the average density of the cells in the container to 100 to 150 cells/ml. The density of inoculum ranged from 1500 to 2000 cells/ml. On occasion less-dense cultures were used, but these caused greater variability in the frequency of occurrence of aggregations and in their longevity. The cells were cultured by William Thomas and staff (Univ. of Calif., San Diego); the technique is described by Thomas et al. (1973). After inoculating the container, we covered it with either a black opaque or a transparent top whereupon aggregations, 5 to 10 cm diameter, formed within 24 h. The container contained only filtered sea water, *Gymnodinium*, and the medium in which the cells were originally cultured. The number of cells in the initial inoculum had a direct effect on the time necessary for the formation of the aggregation and its size. Inoculations that brought the initial cell density in the container to 20 to 80 cells/ml required 24 to 72 h to form aggregations and the aggregations were small, 0.5 to 5.0 cm diameter. When the initial density in the container was only 10 cells/ml, no patches formed after 6 days.

At the initial density in the container of 100 to 150 cells/ml patches formed equally well in constant dark (illumination $\leq 1 \times 10^{-6}$ ft-c) as they did under the fluorescent lamps located above the rearing containers. Distinct aggregations also formed in containers placed outdoors and exposed to direct sunlight. On occasion we used light to establish an aggregation of *Gymnodinium* in a particular position in a container. Once an aggregation had formed, however, it could not be moved to a different position in the container by illuminating a different section of the container. This was the case regardless of whether or not light had been used to establish the patch initially. The only way an established patch could be relocated was by dispersing the patch by stirring and allowing it to re-form. It would re-form in the light or in the dark and usually in a new region of the container. It could also be re-established in a particular region by illuminating one section of the tank. We occasionally used light to relocate an aggregation because we preferred to have the aggregations located near the center of the container. Patches were relocated by stirring the container, and placing an opaque cover over the container with a hole cut in it so that light entered in only one section of the tank. Aggregations, 5 to 10 cm diameter, re-formed after stirring within 3 to 4 h. Relocation of the aggregation was successful 87% of the time (N = 31).

The longevity of *Gymnodinium* aggregations was not measured because the ending of a larval fish experiment required the removal of the patch. During a period of low availability of anchovy eggs, however, of 18 containers inoculated with *Gymnodinium*, all retained aggregations for 10 days and 6 for 16 days.

In summary, the most important characteristics of *Gymnodinium* aggregations were that they were stable, easily detected visually, and formed spontaneously independent of light. The only difficulty encountered was that wind-driven currents sometimes caused the patch to disperse temporarily. This problem was avoided by keeping covers on the containers and turning the air conditioner off before uncovering them.

ATTRACTION OF LARVAE TO PATCHES OF *GYMNODINIUM*

We noticed at the beginning of this study that yolk-sac larvae appeared to be aggregated in patches of *Gymnodinium*. We performed a series of tests to confirm this observation and determine the role that size and density of the patch and the density of cells outside the patch played in the behaviour.

Patches of *Gymnodinium* of various sizes and densities were established in 10 l rearing containers using the methods described in the previous section. We then placed 100 anchovy eggs in each container. The containers in this and all other experiments described in this paper were kept in air conditioned rooms at 17° to 19°C and under light cycles of 14 h light, 10 h dark. On the day the larvae reached the age of 1 day we measured the maximum diameter of the patch and sampled it by selecting an acrylic cylinder similar in size, lowering it over the patch and sealing it with an acrylic plate that had a circular groove cut to fit the cylinder. In such a sample and in control samples we counted the larvae, measured the volume of the water, and measured the density of *Gymnodinium* by counting the cells in ten 0.03, or 0.01 ml samples; the number of larvae remaining in the container were also counted.

Our estimate of the density of the patch was the mean number of cells/ml in the cylinder containing the patch. These estimates were less than the actual density because the patch was most concentrated at the surface and usually did not extend to the bottom of the container. The estimate of the background concentration of *Gymnodinium* was the average of the 4 mean densities taken from the 4 control samples.

Effect of the Volume and Density. We took 27 sets of samples of 1-day-old yolk-sac larvae in containers having patches of different density and volume. A comparison of the percent of larvae captured per unit volume of the sample of the patch to that of samples taken outside the patch showed a difference at $P < 0.00006$ Mann-Whitney U Test (Siegel, 1956). To evaluate the importance of the various characteristics of the patch we plotted the log of the number of larvae captured in the patch against the log of patch density (cells/ml), density outside the patch (cells/ml), patch volume (ml), and number of larvae in the container. The number of 1-day-old larvae in the container varied among tests because of larval and egg mortality and infertile eggs. Consequently, N (the number of larvae present) had to be considered as a variable. Log transformations were used because a better fit was obtained with a multiplicative model than with an additive model.

Partial regression coefficients for number of larvae, patch density, and patch volume were significant ($P < 0.01$), whereas that for the cell density outside the patch was not. That the number of larvae present and patch volume are related to catch is obvious. On the other hand, these variables had to be considered in order to evaluate the effect of patch density. The final multiple regression of larvae caught (C) on the three independent variables - number of larvae present (N), volume of patch (V), and density of patch (D) - yielded the equation

$$C = N^{0.97} V^{0.51} D^{0.58} - 3.969$$

where coefficient of multiple correlation = 0.8493 and the standard error of the estimate = 0.1780. Since the coefficient for N was nearly unity and those for V and D were close to 0.5, the data were fitted to the general equation $C/N = K\sqrt{VD}$, using Marquardt's Algorithm for fitting nonlinear models (Conway, Glass and Wilcox, 1970) giving $K = 0.000208$ with 95% support plane confidence intervals for K of $0.000181 < K < 0.000235$ (Fig. 1). Thus, 1-day-old yolk-sac larvae aggregate in dense patches of *Gymnodinium* and the proportion of larvae attracted is correlated with the density and volume of the patch.

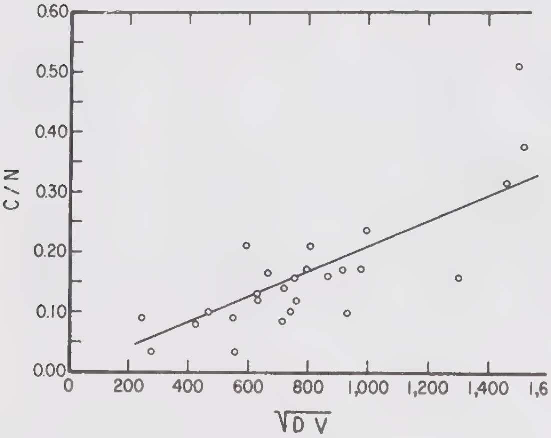

Fig. 1. Relationship between the proportion of 1-day-old anchovy larvae captured in a patch of *Gymnodinium spendens* and the square root of the volume and density of the patch; C/N is the number of larvae in the patch over the total larvae present in the tank; V is the volume of the patch in ml (range, 60 to 850 ml); and D is the density of the patch in cells/ml (range, 540 to 3240 cells/ml). Equation for line is, $C/N = 0.0002\sqrt{DV}$.

We also wished to establish that post-yolk-sac larvae that were actively feeding were also attracted to patches of *Gymnodinium*. For this purpose we made a short series of 11 tests of the same design on 4-day-old larvae. The results, summarized in Table 1, indicate that more 4-day-old larvae were present in the patch than in the first control sample ($P < 0.01$, Wilcoxon matched-pairs, signed-ranks test; Siebel, 1956).

Table 1. Percent of 4-day-old anchovy larvae captured in patch of *Gymnodinium splendens* and in the first of 4 control samples; samples taken during day

Percent of larvae in: Patch of *Gymnodinium*	Percent of larvae in: First control sample	Total larvae	Patch density cells/ml	Patch volume ml
6	8	47	2,085	630
10	6	68	375	580
12	8	72	1,314	710
15	6	52	1,620	680
15	8	52	1,600	610
21	8	77	2,000	600
23	7	87	1,200	750
26	3	92	1,950	600
27	6	67	1,500	600
40	1	183	3,300	800
43	7	56	900	1,000

Effect of Light. The object of this series of experiments was to determine if yolk-sac anchovy larvae continue to aggregate in patches of *Gymnodinium* in the dark and if they could find patches in the dark. In the first of three experiments, we reared larvae from eggs in 10 l containers in which a patch of *Gymnodinium* had been established and sampled the larvae in and out of the patch 6 h after the onset of darkness on the day they reached 2 days of age. In the second experiment, we reared larvae in 1000 ml beakers, added them to 10 l containers in which a patch of *Gymnodinium* was established at the onset of darkness on the day they reached 2 days of age, and sampled the container in the dark 6 h later. In the third experiment we used the same procedure as in the second, except the larvae were placed in the dark for 24 h before taking the samples. In the second and third experiments we added the larvae by submerging the beaker in the 10 l container, a procedure that always resulted in the dispersion of the patch of *Gymnodinium*. Previous tests had shown, however, that the patch would re-form within 3 to 4 h.

All containers were covered with black plastic lids and were kept in a darkened room. At the end of an experiment the lids were removed and samples in and outside the patch taken simultaneously with 9.5 cm diameter cylinders. All containers were stocked with 100 eggs; because hatching rates varied, the number of larvae sampled was expressed as a percentage.

When larvae were associated with the patch of *Gymnodinium* up to the time of capture on the night of age 2 days (experiment 1) more larvae were present in the patch in the dark than in the control sample taken in the dark ($P < 0.01$, Wilcoxon matched-pairs, signed-ranks test). On the average, 24% of the larvae in the container were captured in the patch sample whereas only 4% were taken in the control sample (Table 2). Thus, larvae remained aggregated in the patches of *Gymnodinium* in the dark.

Table 2. Percent of yolk-sac larvae (age 2 days) captured in dark in a sample of a patch of *Gymnodinium splendens* and in a control sample taken simultaneously outside the patch; when the patch was not dispersed, 6 h after dispersion of the patch; and 24 h after dispersion

Percent of larvae in: Patch of *Gymnodinium*	Control sample	Total larvae	Patch density cells/ml
Patch not dispersed			
8	3	58	550
9	0	72	1,830
15	2	57	780
21	1	70	2,380
22	5	43	600
27	0	41	2,560
30	1	89	3,480
31	12	68	2,020
37	10	93	1,630
42	2	103	910
52	8	63	740
6 h after dispersion			
3	7	59	900
3	6	67	450
4	1	103	1,000
5	5	125	1,240
6	1	151	1,000
10	4	67	1,380
16	12	69	1,200
17	3	66	450
19	2	63	1,820
21	12	65	2,280
24 h after dispersion			
13	1	78	1,350
23	8	78	1,110
24	1	95	1,500
26	0	92	1,170
27	3	89	1,410
27	1	85	600
27	0	93	1,770
28	2	82	1,440
28	3	79	1,350
29	4	78	1,620
29	1	106	2,050
30	2	91	1,830
37	2	86	2,220

In the two experiments in which larvae were added at the onset of dark, more larvae were taken in the sample from the newly re-formed patch of *Gymnodinium* than were taken in the control samples ($P < 0.05$ for experiment 2 and $P < 0.01$ for experiment 3 (Wilcoxon matched-pairs, signed-rank test; Siegel, 1956). After 24 h in the dark the percent of larvae captured in the patch was greater than after 6 h in the dark and about the same as in the first experiment. Presence of fewer larvae in the patch after 6 h might be caused by the shorter recruitment period, or because the patches were less dense on the average after 6 h than after 24 h. On the other hand, a long period may be required for the larvae to recover from the disturbance caused by being introduced into the container. It appears that search for concentrations of *Gymnodinium* can proceed on a 24-h basis regardless of the daily changes in light level.

These experiments also show that visual stimuli are not required for finding patches of food. One-day-old yolk-sac larvae have well-developed olfactory organs, and naked neuromasts; but the eyes are not developed. Thus, chemical, acoustic or tactile stimuli could be used by yolk-sac larvae to find concentrations of *Gymnodinium*. A chemical stimulus seems the most likely because algae can produce considerable quantities of extracellular substances (Fogg, 1962; Hellbust, 1965). On the other hand, in post-yolk-sac larvae the search pattern for food could also bring about an aggregation of larvae in areas of high food concentration.

STRUCTURE OF SEARCH PATTERNS

The object of these experiments was to determine how food type and distribution affected the structure of the search pattern of larval anchovy. For this study a large, circular, black fiberglass tank of 122 cm diameter with a 1 cm grid inscribed on the entire bottom was used. We filled the tank to a depth of 18 cm and inoculated it with a prey organism. When the desired food density and distribution was obtained we added eggs or larvae.

We recorded on a key board each time a larva completed a feeding act, when it swam in and out of a patch of *Gymnodinium*, and when it crossed a grid line. A different key was used for each of the four grid directions. If a larva did not move, no event was recorded. Each time a key was depressed the data and the elapsed time to the nearest 0.1 sec were entered on a 8 channel paper tape. The computer output included a plot of movements, swimming speed, frequency of feeding and directional probabilities. Directional probabilities were the proportion of grid intercepts made by a larva that were ahead, to the right, to the left, and backward (a 180° change in direction). Swimming speed was the sum of grid intercepts made by a larva divided by the observation period which was 5 min. It was expressed in cm/sec because the distance between grid lines was 1 cm.

To evaluate how differences in directional probabilities (the proportion of movements made in each grid direction) could affect the area covered by a larva during search we used a computer model of bounded random walks used by Cody (1971) to analyze the movements of bird flocks. The bounds of the walk are boundaries of an 11 X 11 unit grid. The larva is started in the centre and moves only along the sides of 1 X 1 unit squares, one side per step. Directional probabilities were fixed relative to the axis of motion of the larva. For each set of directional probabilities (data from one larva), 100 walks of 200 steps each were made. The results of the simulation included the percentage of possible points which had been visited, the proportion that were visited zero, once, twice, up to 10-plus visits.

Of the statistics generated by the random walk program we used only the percent area covered, the percentage of possible points visited one or more times during the walk for each larva. The percent area covered was considered to be a relative measure of the effect of the directional probabilities on the area searched by a larva. Some may consider its procedure too artificial; thus, in some cases we also compared the directional probabilities of groups directly. This was done by summing the frequencies each larva moved, ahead, right, left, and behind; the sum of the frequencies for each direction for each group of larvae were entered in a contingency table and the Chi-square test was used to determine differences between groups. This procedure inflated the number of observations because the total for each group was the total number of directional movements for the group rather than the total number of larvae observed. We preferred the values from the random walk program because the observations were independent and it indicated the possible effect of directional probabilities on the area searched.

We recorded search patterns and feeding rates of anchovy larvae in patches of *Gymnodinium*, out of patches, and at low densities of *Gymnodinium* where no patches were present. For comparative purposes, search patterns for larvae feeding on the rotifer *Brachionus plicatilis* over more limited density ranges were also studied. In all experiments larvae ranged in age from 4 to 8 days. No difference in behaviour associated with age was detected, so we combined the data for all ages.

Searching Behaviour of Larvae Fed on *Gymnodinium*. Anchovy larvae swam more slowly in patches of *Gymnodinium* ($P < 0.0006$) and fed more frequently than when not in such a patch ($P < 0.0006$ Mann-Whitney U test, Siegel, 1956). Larvae inside a patch swam less frequently directly ahead and more frequently reversed their direction than did ones outside a patch ($P < 0.001$ Chi-square test for two independent samples). The percent area covered, computed by the random walk program from directional probabilities was less for larvae inside a patch than for ones outside ($P < 0.00006$ Mann-Whitney U test). Thus, on the basis of the directional characteristics of the search pattern alone, larvae inside patches of *Gymnodinium* would be expected to cover less area per unit time than ones outside of a patch. The combined effect of the reduction in speed and change in directional probability for larvae in a patch was that ones inside remained within a small area whereas those outside swam over a much greater area.

The change in speed of larvae when they entered or left patches of *Gymnodinium* was abrupt. In 7 observations, the larvae swam in and out of a patch during the 5-min observation period. In all 7, the speed of the larva was higher (median 0.30 cm/sec) when it was outside the patch than when it was inside (median 0.15 cm/sec). Directional probabilities and feeding rates followed the trends described above, but no statistical differences existed - probably because of the small sample size.

The behaviour of larvae in patches of *Gymnodinium* could be a discrete pattern that occurs only when food is at a very high density and sharp boundaries exist; on the other hand, larval searching behaviour may be modified continuously with changes in density and food distribution.

To determine which alternative was the more likely, we divided the data into 3 density classes: 1 to 21 cells/ml; 24 to 260 cells/ml and patch, ≥ 1,000 cells/ml. A plot of the data segregated into the three classes indicated that the speeds and percent area covered for larvae in the 24 to 260 cells/ml class fell between those for larvae in the other two density classes (Fig. 2). This trend is also apparent in the medians (Table 3). The 95% confidence ellipse for these distributions plotted on a log scale also suggest a continuous change in characteristics of the search pattern (Fig. 3). A log transformation was required to normalize the distributions because speed distribution

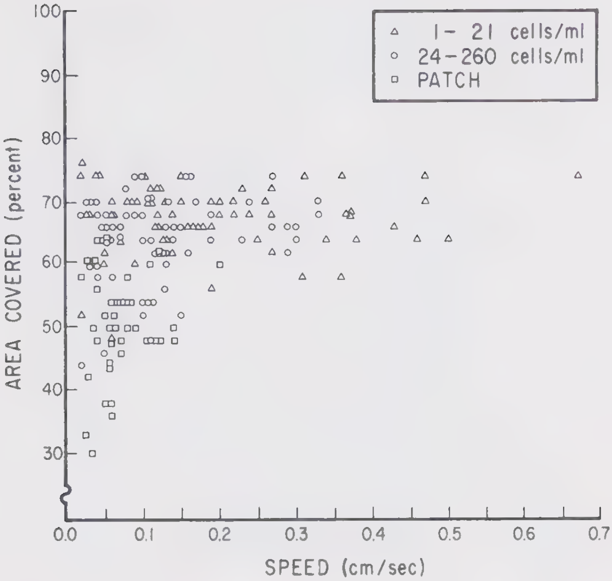

Fig. 2. Percent area covered from random walk program and speed for anchovy larvae 4 to 8 days old fed on *Gymnodinium splendens* at different densities

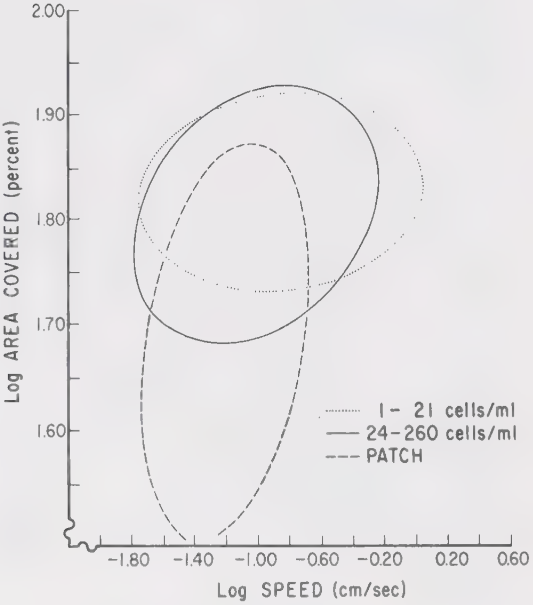

Fig. 3. 95% confidence ellipses for distribution of log of percent area visited on log of speed for larvae fed on *Gymnodinium splendens* at different densities

was strongly skewed. Comparisons of the speed, percent area covered, and feeding rates among the three classes of food density indicated that the distribution of each of these variables in each class was different from that in every other ($P < 0.05$ Mann-Whitney U test). We also compared the directional frequencies directly using the Chi-square test. These tests indicated that the frequency larvae moved in each grid direction differed among the three density classes ($P < 0.001$). From the above evidence we conclude that anchovy larvae responded to the density and distribution of *Gymnodinium* by continual modification

Table 3. Characteristics of search pattern of larval anchovy 4 to 8 days old in different concentrations of *Gymnodinium splendens*, and *Brachionus plicatilis*

Food type	Density range no/ml	N	Median cm/sec	Median feeding strikes/min	Median percent area covered	Mean directional probabilities				Total moves
						Ahead	Right	Left	Behind	
Gymnodinium splendens	1-21	72	0.151	0.00	68.5	0.355	0.311	0.280	0.054	3,821
"	24-260	65	0.105	0.21	65.0	0.319	0.304	0.306	0.071	2,416
"	patch	41	0.058	0.79	49.7	0.161	0.282	0.323	0.234	888
Brachionus plicatilis	10-15	38	0.212	0.86	68.3	0.341	0.305	0.315	0.039	2,465
"	42-72	23	0.162	0.79	65.3	0.324	0.305	0.302	0.068	1,247

of the speed and directional components of their searching behaviour. The result of these modifications was an expansion of searching area at low density and a reduction of the area searched at higher food densities.

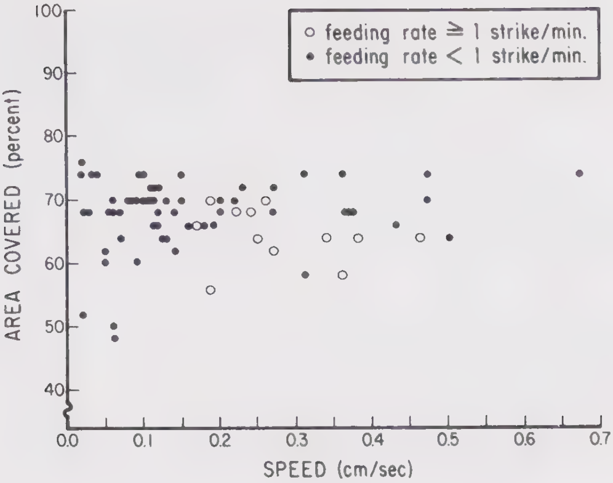

Fig. 4. Feeding rate, speed, and percent area covered for anchovy larvae 4- to 8-days-old fed on 1 to 21 *Gymnodinium splendens*/ml

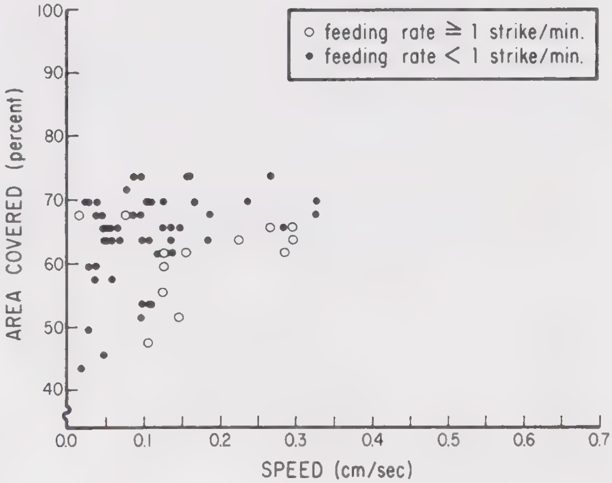

Fig. 5. Feeding rate, speed, and percent area covered for anchovy larvae 4- to 8-days-old, fed on 24 to 260 *Gymnodinium splendens*/ml

Within these classes a relationship existed between speed and feeding rate. Larvae that fed at higher rates tended to swim faster than those that fed less often or did not feed (Fig. 4 and 5). We measured the degree of correlation between feeding rate (completed feeding acts/ min) and swimming speed by calculation of Spearman r_s and Students t associated with that value (Siegel, 1956). In each of the groups a strong positive correlation existed between feeding rate and swimming speed ($P < 0.005$). Thus, within each level the larvae that swam the fastest tended to feed more often, but larvae at lower densities swam faster and fed less often than ones at higher densities.

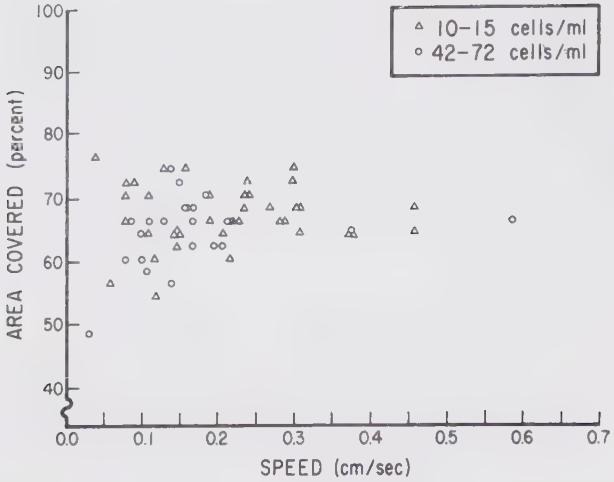

Fig. 6. Percent area covered calculated from random walk program and speed, cm/sec for anchovy larvae 4- to 8-days-old, fed on *Brachionus plicatilis* at different densities

Searching Behaviour of Larvae Fed on *Brachionus*. We used the same techniques and procedures to study the searching behaviour of larvae fed on the rotifer, *Brachionus plicatilis*, as we did for those fed on *Gymnodinium*; however, *Brachionus* was studied over a more limited density range. The data were divided into two density classes, 10 to 15 *Brachionus*/ml and 42 to 72/ml, to determine if density affected any characteristics of the search pattern. The distribution of speeds and percent area covered resembled those for *Gymnodinium* at comparable density levels; the medians were also similar (Fig. 6, Table 3). Comparisons of speed, percent area covered, and feeding rate between the

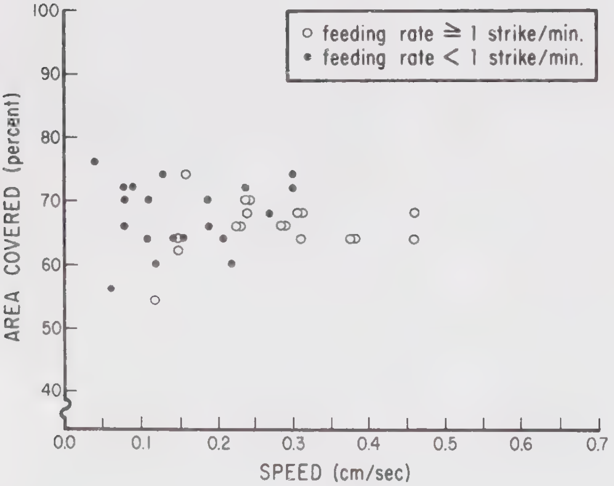

Fig. 7. Feeding rate, percent area covered and speed for anchovy larvae 4- to 8-days-old, fed on 10 to 15 *Brachionus plicatilis*/ml

two density classes of *Brachionus* showed a significant difference only in the case of percent area covered ($P < 0.05$ Mann-Whitney U test). The directional frequencies also differed between the two density classes ($P < 0.01$, Chi-square test).

A tendency existed in both density classes for the larvae that fed at higher rates to swim faster than those that fed at lower rates as was the case for *Gymnodinium* (Fig. 7 and 8). In both density classes of *Brachionus* the association was significant at $P < 0.005$ (Spearman rank correlation, Siegel, 1956).

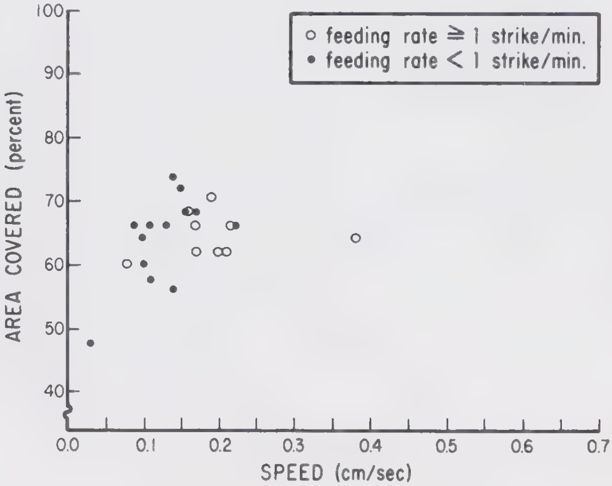

Fig. 8. Feeding rate, percent area covered and speed for anchovy larvae 4- to 8-days-old, fed on 42 to 72 *Brachionus plicatilis*/ml

DISCUSSION

The "non-randomness" of a search pattern of anchovy larvae is in agreement with other findings. Kleerekoper has shown that fish do not move at random in experimental environments that are void of directional cues (Kleerekoper, 1967; Kleerekoper et al., 1970). He also found that the presence of an odor without directional cues caused drastic changes in directional parameters (Kleerekoper, 1967). Beukema (1968) showed that sticklebacks found food in a maze about two times more efficiently than predicted from a random model. The food in the maze was at a lower density than would be expected under natural conditions and the fish improved their efficiency by making fewer reversals of direction than would be expected from the random model. The chance of an immediate occurrence of a reversal in direction was more than doubled when a prey was found. He also pointed out the adaptive advantage of this behaviour for a highly aggregated prey. Wyatt (1972) showed that the time plaice larvae spent swimming increased with a decrease in food density. In our experiments with *Gymnodinium* speed also increased with a decrease in food density and the probability of reversals in direction increased with density when either *Gymnodinium* or *Brachionus* was the prey. The increase in probability of direction reversals, 180° turns, was the principle reason for the decrease in area covered in the random walk at high food densities. We were unable to establish a direct link between reversals of direction and frequency of feeding; but since feeding and reversals of direction both increased with an increase in density they may be related.

The non-randomness of larval anchovy search patterns and the ability of yolk-sac and older larvae to find and remain in concentrations of the dinoflagellate, *Gymnodinium*, are adaptations that should equip them to take advantage of the contagiousness of the distribution of food in the sea. This could be of considerable adaptive significance, depending upon the extent of scale of patchiness of food in the sea. It could explain, for example, why laboratory estimates of food-density requirements of larval anchovy appear to be consistently higher than the average concentrations of food in the sea (O'Connell and Raymond, 1970; Hunter, 1972); and why no difference in mortality of anchovy larvae exists at the onset of feeding in the sea, although their food-density requirement determined in the laboratory is much higher at this time (Lenarz, 1972; Hunter, 1972). Laboratory estimates of food requirements for first-feeding larvae are higher because of their low level of feeding success, and they search a much smaller volume per unit time owing to their small size. If larvae can search for food and remain in concentrations while in the yolk-sac stage, the chance of finding a significant concentration of food before they starve is increased. Anchovy larvae can survive without food for 1.5 days after yolk absorption at temperatures of 22° to 15°C; but if the time to starvation is calculated from hatching, larvae can survive from 3 days at 22°C to 5.5 days at 15°C (Lasker et al., 1970). The variation in times is caused by temperature-dependent differences in the rate of yolk absorption. Since most anchovy eggs are spawned at 13° to 14°C, the time available to find food before starvation is increased 3 to 4 times and this conceivably could counteract the effect of a higher food density requirement.

Also pertinent is the extent that phytoplankton is eaten by larval anchovy under natural conditions. The importance of phytoplankton in the diet of anchovy larvae depends on the availability of patches and on whether or not larvae feed on these organisms in the sea. Phytoplankton form dense patches in the sea. A remarkable example of this is a very extensive bloom observed in the Weddell Sea by El-Sayed (1971).

He recorded densities of phytoplankton of over 2000 organisms/ml for combined species and densities as high as 1700/ml for individual species. These densities are somewhat higher than the ones we typically measured in patches in our containers. Not all species of phytoplankton will sustain life in anchovy larvae, however. To survive, anchovy larvae appear to require that the cells be unarmoured and larger than 30 μ (Lasker et al., 1970). The abundance of phytoplanktonic organisms in the California Current meeting these requirements at the time of spawning of the anchovy is not known. On the other hand, stomach contents of anchovy larvae analyzed by Arthur (1956) indicate that phytoplankton may be of considerable importance in the diet of first-feeding anchovy. 11% of the items he identified in the guts of anchovy larvae 4.5 mm and smaller were phytoplanktonic organisms. If a group Arthur classed as unidentified spheres, presumably unicellular algae 20 μ in diameter is included, then phytoplankton comprised 32% of the diet. We consider 32% a conservative estimate because all organisms Arthur identified had hard parts that could withstand digestion; whereas the cells of a preferred phytoplankter, such as *Gymnodinium*, are broken down very rapidly in the gut and leave no identifiable elements. It should be noted, however, that phytoplankton is probably important for only about the first week of feeding. Lasker et al. (1970) showed that growth of larvae fed on *Gymnodinium* became retarded after about 1 week; Arthur (1956) showed a decline in the percent of phytoplankton in the guts of anchovy larvae with an increase in size. Only 10% of the items in guts of larvae 5.0 to 6.5 mm were phytoplankton and only copepods were present in the guts of larvae larger than 6.5 mm (Arthur, 1956).

SUMMARY

Searching and feeding behaviour of larval anchovy was studied when prey were highly aggregated and at various densities when prey were not highly aggregated. The prey used in most experiments was the dinoflagellate, *Gymnodinium splendens*; the rotifer, *Brachionus plicatilis*, was used in comparative studies.

Yolk-sac and post-yolk-sac larvae were found and remained in patches of *Gymnodinium* in light and in darkness. The number of larvae attracted to a patch depended upon the density and volume of the patch. The structure of searching behaviour at various prey densities was analyzed by recording movements of larvae as they swam over a grid. Speed and direction of search patterns of larval anchovy were density-dependent: larvae swam faster at low prey densities than they did at higher ones; and the expected area covered by a larva on the basis of directional components alone was greater at low prey densities than at higher ones.

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Occurrence, Morphology, and Parasitism of Gastric Ulcers in Blue Marlin, *Makaira nigricans,* and Black Marlin, *Makaira indica,* from Hawaii

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ABSTRACT

Gastric ulcers were found in 10 of 114 blue marlin, *Makaira nigricans,* and 2 of 3 black marlin, *M. indica,* examined from 1967 to 1969 at the Hawaiian International Billfish Tournament. Parasitic nematodes were found imbedded in the base of ulcers in one blue marlin and two black marlin. The gross and microscopic morphology of the ulcers is given and possible causes are discussed. The most likely cause is either mechanical injury or parasites, or the effect of both in the same stomach.

The existence of gastric ulcers in man and other mammals, including marine mammals (Geraci and Gerstmann, 1966) is well known. The existence of gastric ulcers in fish was first noted by Aliverdiev and Radzhabov (1968), Evans and Wares (1972), and Iversen and Kelley (in press). We here report additional details on the occurrence, morphology, parasitism, and possible causes of gastric ulcers in blue marlin, *Makaira nigricans,* and black marlin, *M. indica,* landed from 1967 to 1969 during the annual Hawaiian International Billfish Tournament.

METHODS

One hundred seventeen marlin were captured during daytime trolling in surface or near surface waters just off the west coast of the Island of Hawaii. Each billfish tournament included 5 fishing days during either July or August. Fishing commenced each day at 0800, but the catch was usually not brought to the weighing station until after 1700 when fishing ended, so there often was a lengthy interval between capture and examination of the stomach. After being weighed by tournament officials, each fish was measured, sexed, and examined for stomach contents. Specimens were not refrigerated prior to examination. The estimated maximum interval between capture and examination of marlin containing ulcers was 7.5 h. Histological preparations were by standard paraffin imbedding with hematoxylin and eosin stain.

RESULTS

Ten of 114 blue marlin and 2 of 3 black marlin contained ulcers, for a combined occurrence of 10.3%. Sex, weight, and length for each marlin with ulcers are given in Table 1. Two black marlin and seven blue marlin stomachs with ulcers were preserved in 10% Formalin[3] for laboratory examination. Two of the black marlin and one of the blue marlin stomachs examined in the laboratory contained ulcers invaded by small parasitic nematodes, *Contracaecum* sp.?, a roundworm which has been reported in billfish stomachs from widely separated localities (Wallace and Wallace, 1942; Morrow, 1952).

The following brief comments on gross and microscopic morphology are based upon examination of one of the black marlin stomachs which contained numerous ulcers, both with and without nematodes. The comments are also descriptive of ulcers in blue marlin.

Gross Findings

The ulcers were either separate or in clusters

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[3] Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972.
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Table 1.—Record of marlins with gastric ulcers captured at the Hawaiian International Billfish Tournament, 1967-69.

Date captured	Species	Sex	Wt.	Fork length[1]	Estimated elapsed time, capture to examination
			kg	*cm*	*h*
4 July, 1967	*Makaira nigricans*	F	151.5	303.4	5.5
6 July, 1967		M	141.0	290.0	3.5
29 July, 1968		M	67.6	224.9	6.5
29 July, 1968	*Makaira indica*	F	83.9	240.9	7.5
31 July, 1968		F	86.2	256.1	1.5
1 Aug., 1968	*Makaira nigricans*	M	92.5	256.8	5.0
2 Aug., 1968		M	67.6	230.3	3.0
2 Aug., 1968		F	189.1	315.7	6.5
2 Aug., 1968		F	102.0	270.3	7.5
21 Aug., 1969		M	102.0	268.2	6.5
21 Aug., 1969		M	66.7	236.4	6.5
22 Aug., 1969		M	68.5	235.3	7.0

[1] Tip of snout to center of distal edge of caudal fin.

throughout the stomach (Fig. 1). They were noncancerous. Edges were indurated and raised slightly from the surrounding surface. Ulcer margins were rather sharply demarcated. The bases were covered with a dark brown shaggy material and had an indurated feel. Light gray nematodes 5-7 mm in length and less than 0.5 mm in diameter were imbedded in the bases of four ulcers in this stomach (Fig. 2). The bases of the ulcers were very indurated and the induration extended through the wall of the specimen.

Microscopic Findings

The base of this ulcer was covered by granulation tissue with a dense proliferation of fibroblasts and an infiltration of acute and chronic inflammatory cells (Fig. 3). The fibrous proliferation extended through the entire wall and obliterated the usual muscular layers. Remnants of the nematodes were identified throughout the ulcer base. Generally, there was an intense granulomatosis inflammatory reaction surrounding the parasite. This consisted of inflammatory cells and histiocytes. In some instances the inflammatory reaction had subsided and only laminar layers of fibrous tissue remained (Fig. 4).

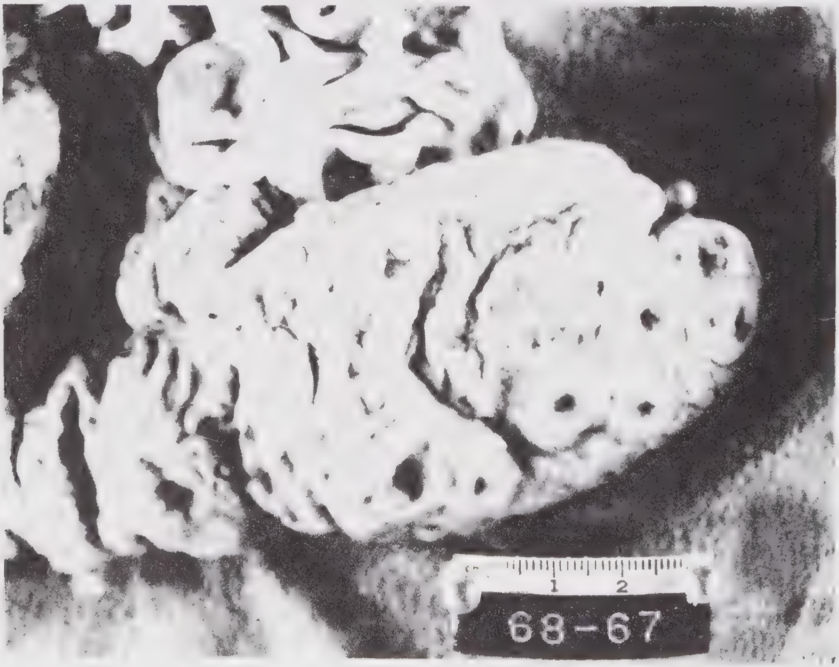

Figure 1.—Multiple ulcerations varying from 3 to 13 mm scattered over the mucosal surface of a stomach from a female black marlin. Weight of marlin 86.2 kg; fork length 256.1 cm.

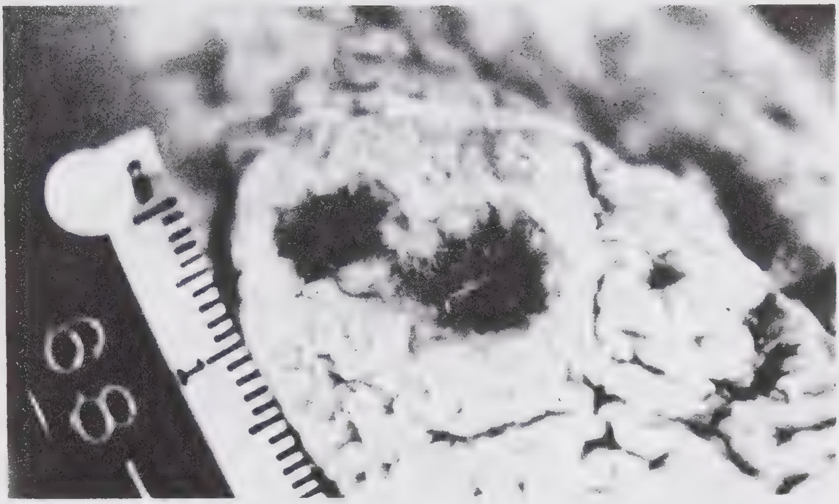

Figure 2.—Closeup view of same black marlin stomach showing nematodes burrowing in base of ulcer.

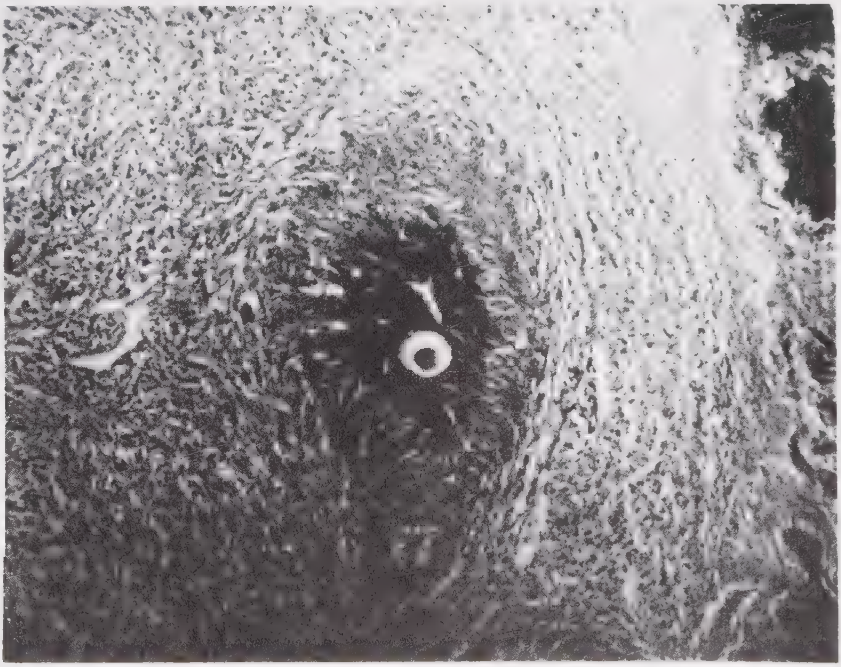

Figure 3.—Microscopic section of base of ulcer from same black marlin showing extensive fibrosis and subacute inflammatory response surrounding portions of nematode sectioned in two areas (H & E stain, 25×).

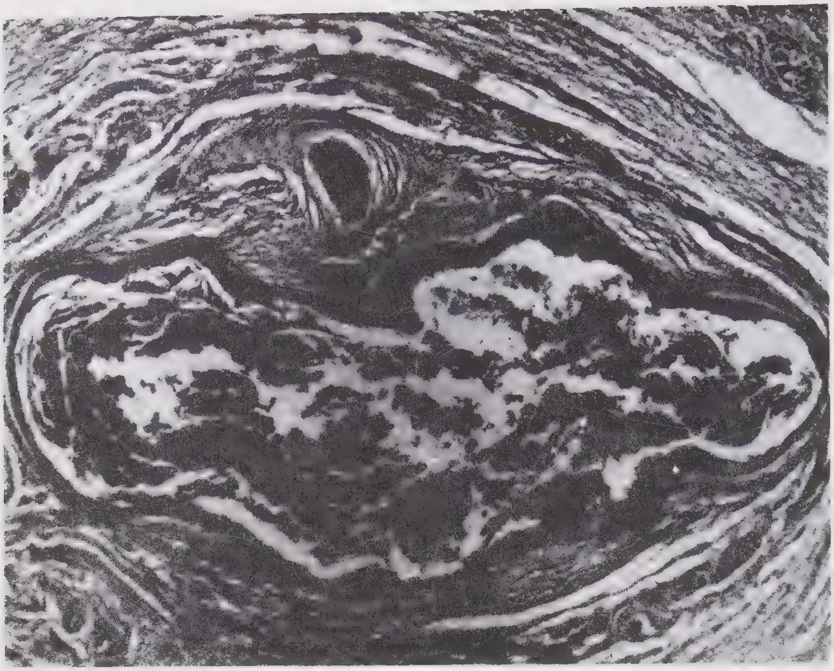

Figure 4.—Microscopic section of base of ulcer from same black marlin showing extensive fibrosis laminated around old nematodal debris (H & E stain, 25×).

DISCUSSION

Several possible causes of the ulcers may be considered. They are (1) mechanical injury to the stomach lining from sharply pointed food items, (2) parasites, (3) digestive processes due to gastric secretions between the time of death and time of examination, and (4) excess gastric secretions.

The most likely cause is either mechanical injury or parasites, or the effect of both in the same stomach. Blue and black marlins feed heavily on fish, many having sharply pointed projections. Examples are the dorsal spines of skipjack tuna, *Katsuwonus pelamis,* and yellowfin tuna, *Thunnus albacares.* Both of these tunas are commonly eaten by marlins. We have recovered a sliver of bonelike material from beneath the epithelium of the stomach of a marlin captured during a billfish tournament. Other examples are the spiny puffers, Diodontidae, which sometimes occur in marlin stomachs. Spiny puffer remains were found in one of the stomachs containing an ulcer, and it is possible that multiple punctures of the stomach lining could occur after engulfment of such food. Multiple punctures could also be caused by engulfment of prey items with sharp spines during successive feedings. This could explain instances of multiple ulcers in some of the marlin stomachs. For example, the black marlin stomach shown in Figure 1 had six ulcers wider than 10 mm and over 50 smaller ulcers less than 10 mm wide.

Evans and Wares (1972) reported finding gastric ulcers in 14% of 563 striped marlin, *Tetrapturus audax,* and 22% of 151 sailfish, *Istiophorus platypterus,* examined in Mexican and southern California waters in 1968. They did not, however, cite the presence of nematodes, either in stomachs with or without ulcers. They also suggest spines of prey species may have caused the ulcers.

In those ulcers containing nematodes, it is uncertain if the ulcers were caused by the nematodes, or if the nematodes took advantage of the ulcer and burrowed inward. Other workers have found a high percentage occurrence of nematodes in marlin stomachs without citing the presence of ulcers. Wallace and Wallace (1942) found *Contracaecum incurvum* in 60 of 86 stomachs of white marlin, *T. albidus,* captured off Ocean City, Maryland. Morrow (1952) reported finding *C. incurvum* in each of 53 stomachs of striped marlin, *M. mitsukurii* (= *T. audax*), from New Zealand. If this nematode causes ulcers, its association with ulcers should be common, which is not the case, according to published reports. This implies mechanical injury is the most likely cause, with the ulcers being further aggravated in those stomachs containing parasitic nematodes.

Digestive action by gastric secretions after death is another possibility, but it seems highly unlikely the large size of some ulcers could develop even during the lengthy interval between capture and preservation of the stomach. For example, the 83.9 kg black marlin captured in 1968 had one ulcer that was 40 mm long, 27 mm wide, and 10 mm deep (measurements after preservation in Formalin). In addition, 30 nematodes and necrotic tissue were present in the pit of this ulcer.

High concentrations of free circulating histamine might possibly cause ulcers by increasing gastric acid secretions. It is known that histamine has an ulcerogenic effect on warm-blooded animals (Hay et al., 1942). Geraci and Gerstmann (1966) have suggested that histamine from a diet of inadequately preserved fish caused gastric ulcers in a captive bottle-nosed dolphin, *Tursiops truncatus*. Fresh fish contain negligible amounts of histamine, but under conditions of inadequate preservation, decarboxylation results in the formation of histamine from histidine (Geraci and Gerstmann, 1966). Since marlin feed on fresh fish, it seems unlikely much of the prey's histidine may find its way into the marlin's blood stream as histamine. Further, the effect of histamine on gastric secretions in teleosts is unknown. In the spiny dogfish shark, *Squalus acanthias,* perfusion of isolated gastric mucosa with histamine resulted in an increased secretion of acid 1 to 1.5 times the amount secreted by isolated dogfish gastric mucosa not perfused with histamine, but high concentrations of histamine were required (Hogben, 1967).

Increased gastric secretion from behaviorally induced stress conceivably might have an ulcerogenic effect on marlin. The average sex ratio of blue marlin landed during Hawaiian International Billfish Tournaments from 1962 to 1972 has been 3.3 males:1 female, while blue marlin caught by commercial fishing in subsurface waters in Hawaii have an almost 1:1 sex ratio (Strasburg, 1970). It has been suggested the unequal sex ratio of blue marlin caught during the tournaments may indicate a spawning aggregation. Such an aggregation conceivably might be stress-inducing but this is highly speculative and probably unrelated to ulcer occurrence. Adequate data on the sex ratio of black marlin are not available.

ACKNOWLEDGMENTS

We gratefully acknowledge the cooperation of anglers and officials of the annual Hawaiian International Billfish Tournament in making these specimens available for examination.

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MFR PAPER 1091

Improved handling and development of new uses will be the key to the red crab fishery.

Development of the Pelagic Red Crab (Galatheidae, *Pleuroncodes planipes*) Fishery in the Eastern Pacific Ocean

SUSUMU KATO

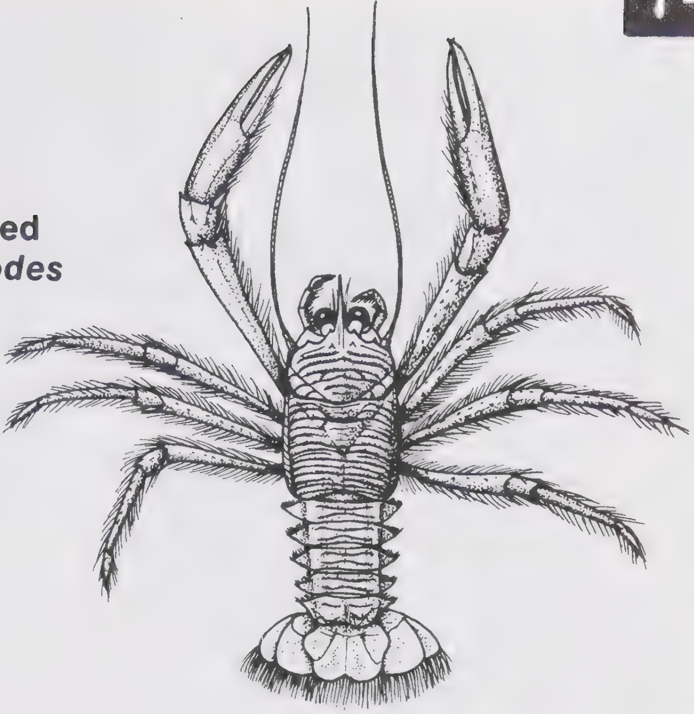

Figure 1.—The pelagic red crab, *Pleuroncodes planipes*. Overall length is about 3.5 inches. (From Boyd, 1962.)

INTRODUCTION

Recent fishing trends demonstrate that the oceans may not contain an inexhaustible supply of fishes. Many of the major fisheries of the world have reached their peaks and several have declined because of decreasing populations. Thus, more and more the fishing nations have turned to previously unutilized resources, and to aquaculture, to satisfy an ever increasing demand for marine products.

Many species of fish and other marine organisms remain unutilized because knowledge is lacking about their distribution and abundance, or owing to a lack of technological capability to harvest and process them economically. As new harvesting and processing methods develop, concurrent with accumulation of knowledge about new resources it becomes possible to utilize previously unused species. Thus, for example, the Japanese and Russians have started fisheries for the small shrimp-like euphausiid ("krill") which is abundant in Antarctic waters (Lyubimova, Naumov, and Lagunov, 1973).

Another large crustacean resource is the pelagic red crab (*Pleuroncodes planipes*) found off the western coast of Mexico, especially near Baja California. (This species should not be confused with the deep-sea red crab, *Geryon quinquedens*, of the Atlantic coast.) Recently American fishermen, with the aid of the National Marine Fisheries Service (NMFS) and the Mexican Government, have started commercial utilization of the pelagic red crab. This paper summarizes the biological information on red crabs and the evolution of the fishery.

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DESCRIPTION

The pelagic red crab, *Pleuroncodes planipes* Stimpson (Fig. 1), is a member of the crustacean family Galatheidae, a group of small, lobster-like crabs. Boyd (1962) points out Stimpson's humorous intent in deriving the name *Pleuroncodes planipes*, which translates to "bulgy-sided crab with flat feet." Galatheids typically have abdomens and tail fans well-adapted for swimming, and their long first pair of legs is armed with pincers (chelipeds) (Schmitt, 1921). Rows of hair-like setae are located on the front and hind margins of the walking legs. Their probable function is discussed later.

Adult red crabs are about 3.5 to 5 inches long, with the tail and chelipeds extended (Fig. 2). A pound of red crabs includes about 100-150 adult individuals. Their color ranges from pale orange to bright red; brilliance of their color may depend in part on ambient light conditions.

LIFE HISTORY

Each female may have two and sometimes three broods of eggs in one season. Females may carry up to 3,650 eggs which hatch after about 2 weeks (Boyd, 1962).

In the laboratory, crabs have passed through five larval stages in from 2 to 4 months (Boyd, 1960), the length of time depending primarily on the temperature of the culture medium. The young crabs lead a planktonic life for about a year (Boyd, 1962). Sometime during their second year, crabs become reproductively mature and spend time on the bottom as well as in the plankton. By this time the crabs are about 0.6 inch long[1] (Boyd and Johnson, 1963). By the end of the second year the crabs become strictly benthic at a size of about 1.02 inches (Boyd, 1962).

Principal spawning grounds for red crabs probably are inshore near

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[1] The 0.6-inch carapace length, measured from the base of the large spine at the front of the head to the posterior margin of the carapace, is used as the standard measurement throughout this paper.

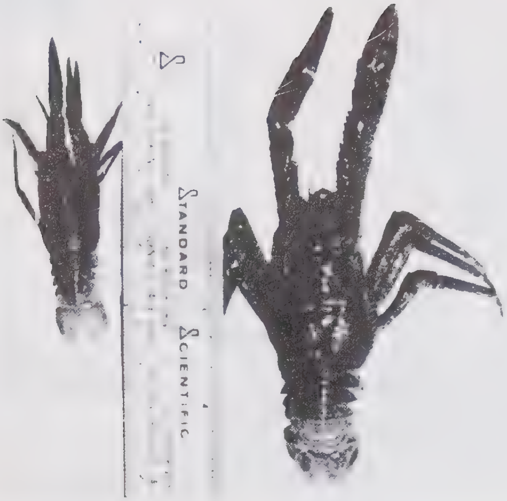


Figure 2.—Adult red crabs.

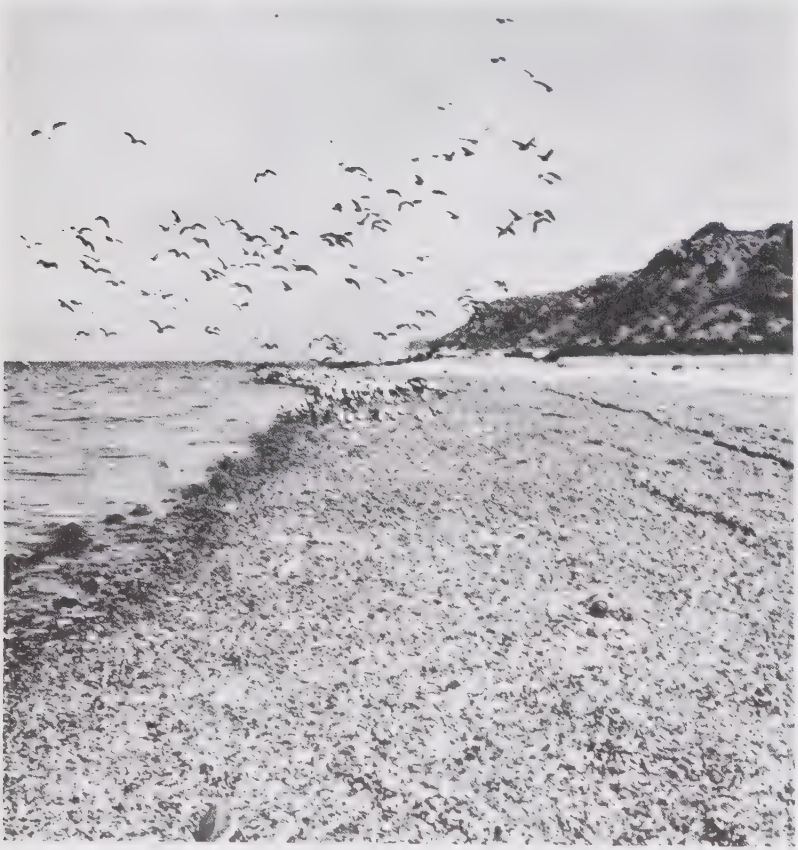


Figure 3.—Dead crabs strewn on the beach at Bahia Magdalena.

southern Baja California, especially in the region of Bahia Magdalena (Boyd, 1960). Katsuo Nishikawa, Escuela de Ciencias Marinas, Ensenada (pers. comm.), reported finding dense concentrations of megalop larvae, presumably of red crabs, while skin diving in Bahia Magdalena. Breeding also occurs far offshore (Longhurst and Seibert, 1971), and during certain years as far north as southern California. Probably these crabs have difficulty returning to the inshore environment, although subsurface currents could possibly aid their migration (Longhurst, 1968a).

The primary breeding season for red crabs appears to be from January through March (Boyd and Johnson, 1963), but I have seen berried females in late October, and young larvae have been found during other months. In the laboratory, the egg-bearing season was November through April, with a peak in February (Boyd, 1962).

Larvae of most Galatheids are planktonic (carried passively by currents), and adults are usually benthic (live on the bottom). Adults of *Munida gregaria*, an Antarctic species, however, occasionally swarm in midwater or at the surface (Matthews, 1932). Red crabs are unique in that they spend a considerable part of their adult life both on and off the bottom and may well interchange these different life styles as conditions dictate (Boyd, 1967). The term "pelagic," usually referring to strong swimmers, has been applied to red crabs found off the bottom, but with the understanding that currents play a major role in their distribution and movements. Crabs larger than about 1 inch in carapace length, probably 2 years old, appear to be strictly benthic and live in deeper waters of the continental shelf (ibid).

Boyd (1967) found significantly higher catch rates of red crabs in plankton hauls at night than during the day. He attributed the difference to upward migration from deeper water at night and the reverse during the day. Crabs caught at night were generally larger, as were those caught at higher latitudes.

The habit of swarming at the surface makes red crabs conspicuous to ocean travelers. These swarms are apparently not associated with seasonal (winter) breeding cycles (Boyd, 1967). Windrows of crabs at the surface sometimes stretch for miles like a blood-red river. Such concentrations occur more commonly at night, but are also evident during the day (Boyd, 1962). Mass mortalities occur when the pelagic red crabs are carried to shore by winds, waves, and currents (Fig. 3).

FEEDING AND PREDATORS

Red crabs are omnivorous and quite versatile in their food habits. When kept in aquaria they feed readily on fish, using their chelipeds to break off small pieces of flesh. They also use the chelipeds to capture small prey like copepods (Longhurst, Lovenzen, and Thomas, 1967). They are unusual in that they can also feed directly on microscopic plants and animals (plankton) by filtration. Analyses of stomach contents of red crabs reveal that the pelagic phase feeds primarily on small phyto- and zooplankton (Longhurst, et al., 1967; Beklemishev, 1960).

In the wild, red crabs can be observed swimming backward and upward by rapidly flexing their abdomens. At or near the surface they stop swimming, stretch out all their legs—thus creating a parachute effect because of the numerous fine hairs on the legs—and float slowly downward while using their filtering mechanism to feed (Fig. 4). Benthic red crabs probably feed primarily on detritus by raking up sediments with their feet and mouth parts (Boyd, 1962).

Beklemishev (1960) described a peculiar behavioral pattern of red crabs which may be related to feeding. About one-third of the red crabs he observed swam upside down, and the majority of these crabs appeared to maintain themselves at the surface by hanging on the surface film with their legs, presumably feeding on surface plankton.

Predators of red crabs are many and varied. Wherever they are found, red crabs are eaten by skipjack tuna, yellowfin tuna, and albacore (Alverson, 1963; McHugh, 1952), many other species of fishes, several species of birds, sea lions (Boyd, 1967), and some whales (Matthews, 1932). Because of their ability to feed on phytoplankton, red crabs form an important and rather direct intermediate link in the food chain from primary productivity to terminal predators (Longhurst, et al., 1967).

DISTRIBUTION

The distribution of the pelagic or planktonic phase of red crabs has been well-documented (Boyd, 1967; Longhurst, 1967, 1968a; Blackburn, 1968, 1969). Generally, the center of distribution is near the west coast of central and southern Baja California. The dominant California Current carries some crabs far out to sea as it swings offshore from southern Baja California. Red crabs have been found over 1,000 miles from the Baja California coast and in two instances were also reported from Central America and Peru (Longhurst and Seibert, 1971). Although the pelagic distribution is widespread, dense concentrations are few; the region of greatest abundance is over the continental shelf off southern Baja California (Fig. 5A). Distribution and abundance of red crabs along the coast appears to correspond to the plankton-rich waters derived from coastal upwellings (Longhurst, 1967; Blackburn, 1969).

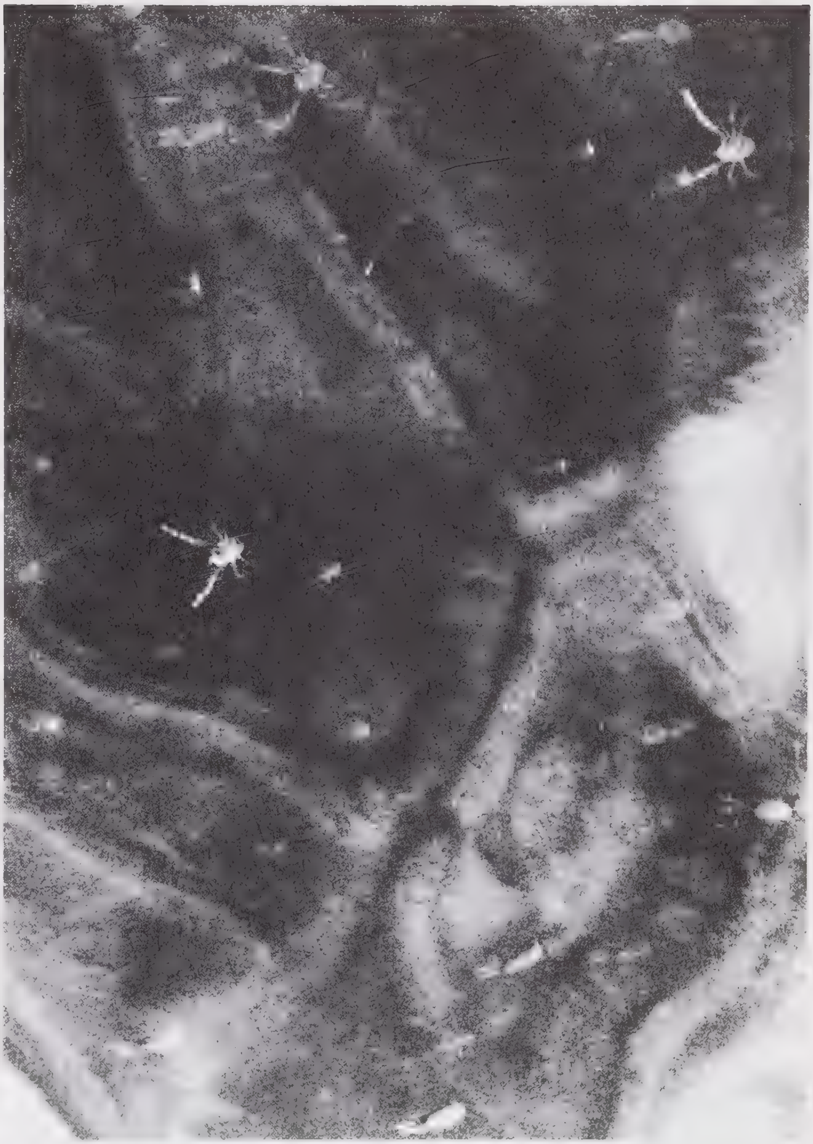


Figure 4.—Red crabs swimming and feeding near the surface. Crabs with outstretched legs are slowly drifting downward, while those with chelipeds extended in front and abdomens flexed are swimming upward.

Large concentrations of red crabs have also been reported from the northern part of the Gulf of California, and mass strandings have occurred on beaches there (Boyd, 1967; Cadieux, 1973). Whether these crabs form a population separate from those off the west coast of Baja California is unknown.

Seasonal variation in distribution apparently is slight, but annual variations may be great (Longhurst, 1967). During certain years, strong north-

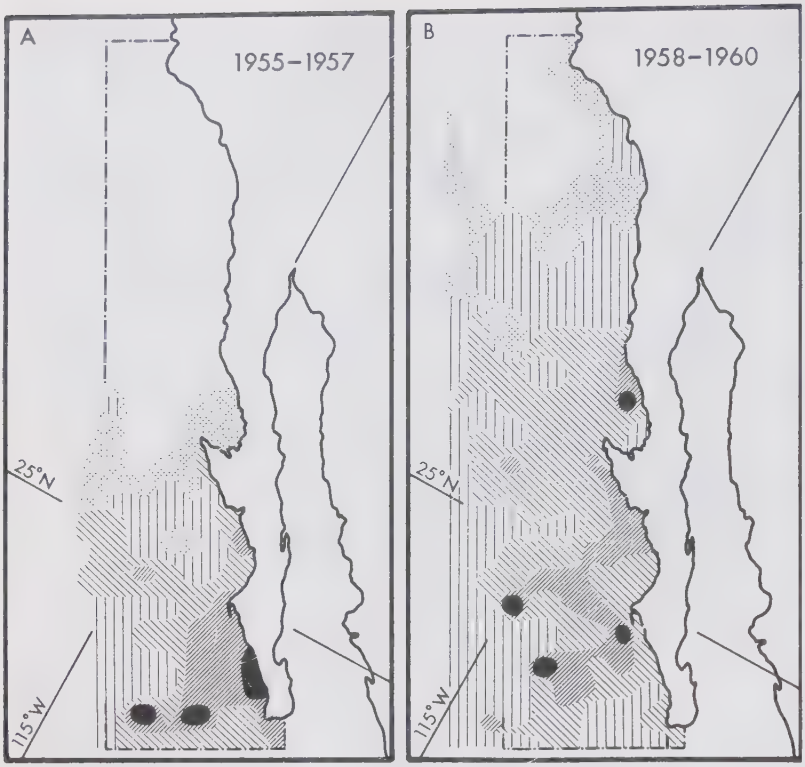


Figure 5.—General distribution of pelagic red crabs along the Baja California and California coasts. Darker shading indicates heavier concentration. A: Normal year. B: Warm year. (From Longhurst, 1967.)

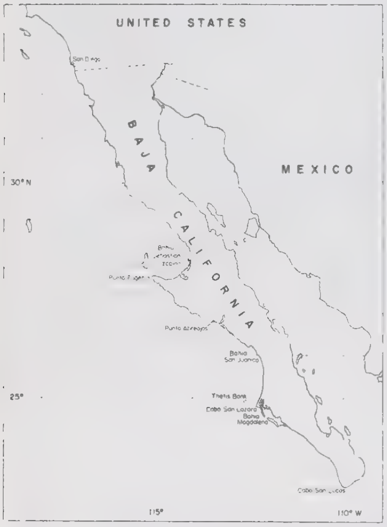


Figure 6.—Map of Baja California, showing important landmarks on the west coast.

ward transport of water along the west coast carries red crabs to southern California and occasionally as far north as central California (Fig. 5B). The period 1958-60 saw this happening, and most recently during the summer of 1972, red crabs were caught in large numbers with a midwater trawl at the Channel Islands near Los Angeles by the California Department of Fish and Game (Kenneth Mais, Dept. Fish and Game, 350 Golden Shore, Long Beach, Calif., pers. comm.). Red crabs were evident off southern California throughout the rest of the year and into the spring months of 1973. Several mass strandings of red crabs occurred on coastal beaches near Los Angeles and the Channel Islands. Commercial fishermen reported large numbers in the water and in the stomachs of fishes that they caught. Red crabs were also found near Monterey, Calif. during spring of 1973 (Jerome Spratt, California Dept. Fish and Game, 2201 Garden Rd., Monterey, Calif., pers. comm.).

Red crabs are found mostly in 59-70°F seas, but have also been found in temperatures of 48-82°F (Longhurst, 1967). Crabs found in offshore areas are generally smaller than those found close to shore. This suggests that they may have originated in inshore waters but were swept offshore as larvae. However, since egg-bearing females about 0.5 inch in carapace length have also been found offshore, it is likely that at least some red crabs are hatched in offshore waters (Longhurst, 1967). Examination of samples taken between 1958 and 1960 indicated that more male than female red crabs occur in the plankton (Boyd and Johnson, 1963). The sex ratio for the entire time period was about 54:46 in favor of males.

Larvae of all stages are found in the plankton from January to July, with the peak in February and March (Boyd, 1960). The greatest concentration was found within a radius of 50 miles of Bahia Magdalena (Fig. 6). In this area, up to 42,000 larvae per 1,300 cubic yards of water were caught in plankton nets, while outside the area during the same period (January through July) the average catch was only five larvae per 1,300 cubic yards.

Unlike the pelagic environment, the benthic habitat of red crabs has not been extensively surveyed. For several years, scientists of Scripps Institution of Oceanography (SIO) have occasionally conducted cruises in inshore waters of central and southern Baja California using otter trawls to capture benthic fishes. At times the presence of red crabs made it impossible for SIO personnel to trawl for fishes (Don Dockins, SIO, La Jolla, Calif., pers. comm.). Red crabs were caught from Bahia Sebastian Vizcaino to Cabo San Lucas. Depths of the areas trawled were generally between 30 and 100 fathoms.

Parker (in Longhurst, 1968b) found benthic red crabs as far north as Bahia Sebastian Vizcaino (about lat 28°N), which appears to be the northern limit of the crabs, except during warm years when both benthic and pelagic phases are found off California. The greatest depth at which red crabs were found was 200 fathoms. Perkins (ibid) reported that the crabs were extremely abundant in waters deeper than 80 fathoms.

In November-December 1960, Boyd (1967) used a small otter trawl to sample the bottom from about lat 25° N to 31°N. No red crabs were found north of Punta San Eugenio (lat 27°

Table 1.—Proximate composition of uncooked red crabs.

Moisture	76.89%
Total Crude Protein	10.61%
Total Lipid	2.48%
Ash	6.29%
Iodine No. of Fat	175
Crude Fiber (Chitin)	5.00%
Salt (NaCl)	1.25%
Volatine Acid Number	16.8
Volatile Base N	0.03%
pH	6.88
Total Carbohydrate (as glucose)	0.94%

Table 2.—Composition of cooked and uncooked red crabs.

Composition	Cooked	Uncooked
	Percent	
Total solids	16.9	23.4
Total lipids	0.8	3.0
Ash	6.2	8.2

Table 3.—Material balance of cooked and uncooked red crabs after passing through a meat/shell separating machine.

	Cooked	Uncooked
Wt of crabs	26.6 lb	29.5 lb
Wt of discarded shell	8.4 lb	13.2 lb
Wt of meats & viscera	17.8 lb	8.8 lb
Physical loss	0.3 lb	7.5 lb
Percentage yield	67.0	30.0

Table 4.—Composition of cooked and uncooked red crab meat and viscera fraction.

Composition	Cooked	Uncooked
	Percent	
Solids	12.9	16.3
Lipid	1.0	3.8
Ash	3.7	3.3

Table 5.—Composition of protein concentrate prepared from meat and viscera.

Composition	Cooked	Uncooked
	Percent	
Protein[1] (N × 6.25)	61.4	59.3
Lipid	0.05	0.05
Ash	23.3	24.8

[1] Not corrected for chitin.

50′N). During a cruise in April 1961, he found crabs south of lat 24°N. In running a transect of trawling stations from near shore to the edge of the continental shelf, Boyd found red crabs between 41 and 164 fathoms. At the latter depth, the crabs measured an average of 1.10 inches carapace length, with a maximum of 1.26 inches. These crabs were presumed to be strictly benthic, because no crabs over 1.02 inches were found in the plankton or in bottom samples from shallower areas. Boyd also suggests that in shallow waters, crabs which are planktonic at night may settle on the bottom during the day when suitable bottom is available.

A cruise in April 1973 by SIO discovered that red crabs are abundant as far south as Costa Rica (Don Dockins, SIO, La Jolla, California, pers. comm.). Between about lat 11-12°N, at depths of about 60-100 fathoms, the crabs were numerous enough to cause problems in retrieval of the bottom trawl used, and subsequent separation of desired fish specimens from the crabs.

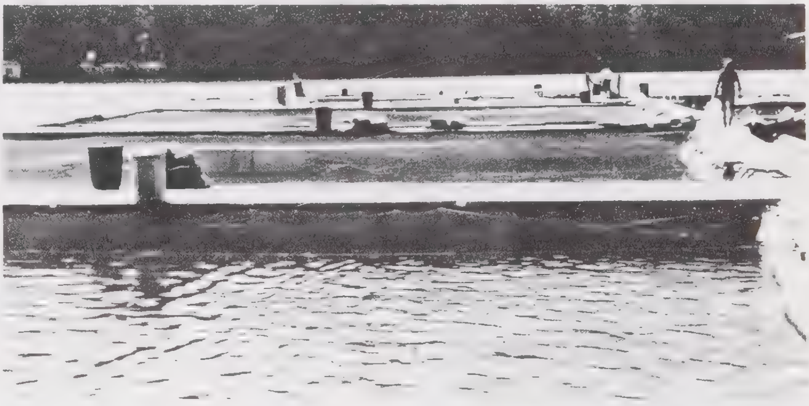
ABUNDANCE

Because very few quantitative data are available, no estimate of the total abundance of red crabs can be made. The catch with a small (10-foot headrope) otter trawl towed for 25 minutes at 2 knots was about 400-500 pounds (Boyd, 1967). Thus a conventional shrimp trawl (55-foot headrope) would be expected to catch about 2,500 pounds under similar conditions.

Beklemishev (1960) calculated that there were more than 300,000 tons of red crabs in an area of about 77,000 square miles off Baja California which was surveyed by the Russian research vessel *Vityaz* in January 1960. Based on catch rates aboard the NMFS research vessel *David Starr Jordan* catches up to 20 tons an hour could be expected with a 50-foot midwater trawl (National Fisherman, 1970). It is clear that in areas where red crabs are concentrated, the catch rate is limited only by the size of the gear that a vessel can handle. It should be pointed out, however, that concentrations yielding such high catch rates are not found throughout the range of the species.

Longhurst (1968b) suggested that the four million yellowfin tuna caught by the United States and Mexican fishery off Baja California in 1960 consumed 2,000 tons of red crabs each day. It is evident, however, that a decimal point was misplaced in his

Figure 7.—Salmon-rearing pens located at Squaxin Island, Washington. (Photo by J. Frazer, STOWW.)



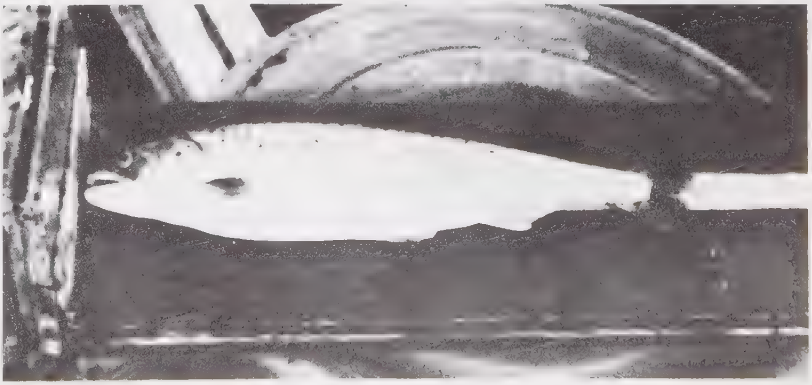


Figure 8.—Pan-sized salmon ready for market. (Photo by J. Frazer, STOWW.)

calculation because the data on which that estimate was based showed that the 567 yellowfin stomachs sampled contained a total of 30.9 quarts of red crabs (Alverson, 1963), which amounts to 0.05 quarts per fish rather than 0.5 quarts as indicated by Longhurst. Thus his estimate is too high by a factor of 10. However, when one considers the consumption by the entire population of yellowfin, as well as skipjack and scores of other predators which feed on the crabs, it is evident that the stock of red crabs is huge.

UTILIZATION

The abundance of the red crab resource has been common knowledge to the fishing industry for years. However, no attempts were made to develop uses for the crabs, principally because of the small amount of meat in the tail. To explore possible uses, NMFS ran a series of analyses on red crabs to provide potential users with basic data. Tables 1-5, reported previously in National Fisherman (1970), give results of these analyses by NMFS and by a private firm.

The results attracted the attention of a pet food manufacturing firm which decided to explore the possibility of including the crabs in a special pack. Accordingly, it ordered a sample shipment from Matt May, then owner of the vessel *American Eagle*, and the commercial fishery was born. Fifteen hundred pounds of red crabs—enough for studies on consumer (cats) acceptance—were caught during the first trip in July 1970. NMFS provided the gear for catching the crabs, and the author went along to study the crabs and fishing operations.

Meanwhile, the NMFS's Northwest Fisheries Center in Seattle discovered that when red crabs were included in the diet of pen-reared Pacific salmon (*Oncorhynchus* sp.), the flesh gained its natural reddish tint (Anthony Novotny, NMFS, Northwest Fisheries Center, pers. comm.). Without the crabs, the flesh remained white. Carotenoid pigments, which red crabs contain in quantity (Wilkie, 1972), caused this effect. Earlier efforts to induce red-colored flesh included feeding the salmon with various sources of carotenoid pigments, and even paprika. The salmon-rearing industry has grown dramatically recently (Fig. 7 and 8) and the production from three private firms was projected to reach 4-5 million pounds by 1974 (Wagner, 1972).

Red crabs were sorely needed for further research, and the California Department of Fish and Game's research vessel *Alaska* provided two oneton loads. The crabs were used primarily by the NMFS's Pacific Fishery Products Technology Center in Seattle to study characteristics of red crabs pertaining to handling and storage aboard fishing vessels. Studies of the effects of the crabs in the diet of rainbow trout brood stock were also begun at the University of Washington.

Late in 1972 the Small Tribes Organization of Western Washington (STOWW) requested aid from NMFS in getting a supply of red crabs for feeding pen-reared salmon. STOWW is a service organization providing economic, social, and administrative services to the membership of 18 Indian tribes. Red crabs had been present in southern California waters since summer, and in early 1973 they were still being stranded on beaches while fishermen reported large numbers near the Channel Islands. Brent Bixler, owner and captain of the fishing vessel *Lady Olga*, agreed to try fishing for red crabs for STOWW after learning of the potential growth of the fishery. In February, equipped with both large and small midwater trawls loaned by NMFS, *Lady Olga* fished for 4 days at the Channel Islands. Total catch was a disappointing 500 pounds of crabs, but valuable experience was gained.

Since red crabs are distributed primarily near Baja California, the Mexican Government was petitioned to allow *Lady Olga* to fish for crabs in Mexican waters. Owing to the experimental nature of the fishery, Mexican officials granted the *Lady Olga* their permission in exchange for data on all aspects of the fishery. Thus on 11 April 1973, the vessel left San Diego to launch the fishery in earnest. Besides Bixler, crewman Dave Johnson, and the author, Mario Yoshida, a student from the Escuela Superior de Ciencias Marinas in Ensenada, Mexico, went along as official observer for the Mexican Government.

Fishing operations started at Punto Abreojos (lat 26°45′N; 113°40′W) where Fathometer[2] readings and visual sightings indicated the presence of red crabs. The first sign of large numbers of crabs near the surface was in waters discolored by a bloom of plankton, probably *Gonyaulax*, an organism which produces the widely known "red tide." Many crabs were seen repeatedly swimming to the surface and then sinking slowly, then swimming upwards again. Undoubtedly the crabs were feeding on the concentrated plankton. Boyd (1962) also reported red crabs associated with

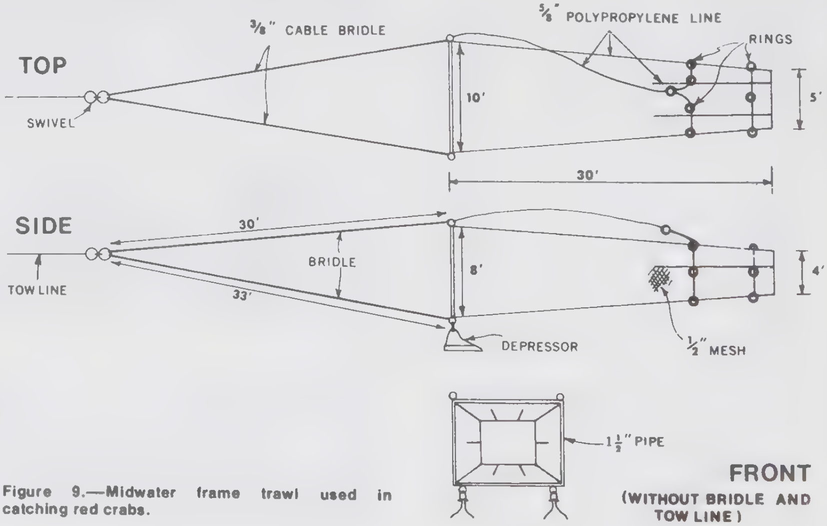


Figure 9.—Midwater frame trawl used in catching red crabs.

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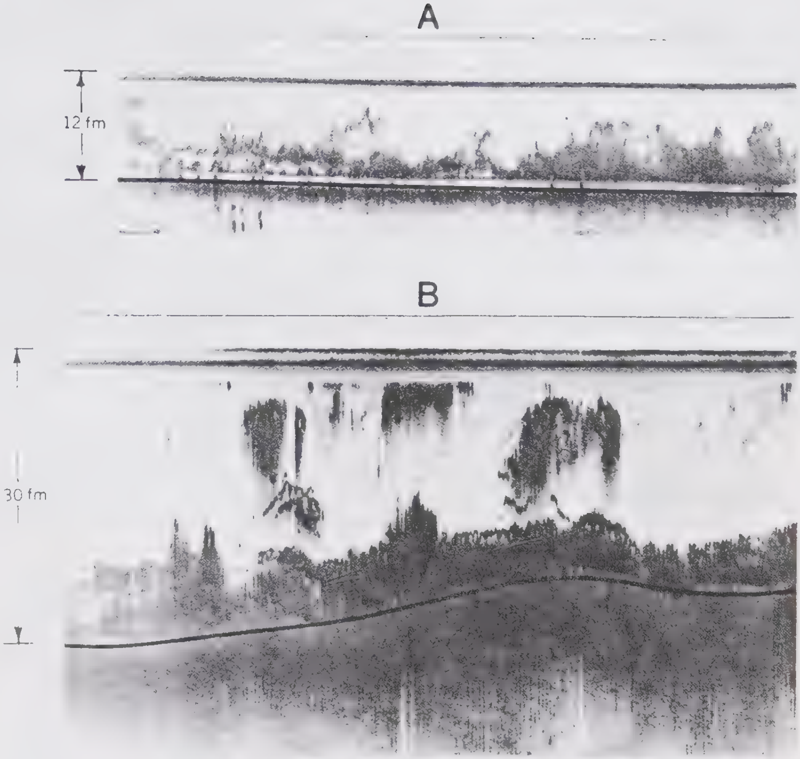
[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



crabs on a "white line" Fathometer. A: Bahia Magdalena. Crabs on and near bottom. The inverted "V" traces were probably fish. B: Thetis Bank. Crabs on the bottom as well as near the surface. The "white line" is occluded because of the density of the crabs.

Gonyaulax, which produces toxins fatal to many fishes and invertebrates. Apparently the crabs are immune to the toxins.

A few days of fishing near the area proved that commercial quantities were not present. For this trip a midwater frame trawl with an 8 × 10-foot opening was constructed (Fig. 9). The webbing was simply attached to the four sides of the frame and tapered to an end opening half the size of the mouth. A conventional cod end was not sewn into the end. A pair of 40-pound depressors kept the opening vertical during tows. The net worked satisfactorily in catching crabs, but bringing the crabs aboard proved difficult because the webbing was too light, and reinforcing rib-lines were insufficient to hold the weight of the crabs.

Following 4 days of unproductive searching and fishing, we entered Bahia Magdalena. Several Mexican shrimp vessels were anchored in the bay, and we learned from their crews that crabs were so abundant in the bay that at times it was impossible for them to trawl for shrimp. A couple of hours of scouting confirmed their reports. The Fathometer showed dense traces (Fig. 10) and hundreds of birds sat on the water feeding on red crabs, while others flew over the water and neatly picked up crabs at the surface.

Fishing began the next day, and by the end of 5 days the hold was filled with 42,600 pounds of red crabs (Table 6). Much time was lost owing to inadequacy of the net. The catch rate could easily be doubled with the proper net. Because the crabs had to be shoveled into plastic bags before being placed in the refrigerated fish hold, handling and storage was also time-consuming and laborious, and 6-8,000 pounds were about maximum for a 15-hour workday.

Several behavioral characteristics of red crabs and birds were learned which proved useful in finding the crabs. The crabs do not stay in the identical area from day to day. They may move both along the shore and slightly offshore or inshore. They often stayed very close to the bottom during the day (thus making it difficult to use a midwater trawl), and moved up somewhat during the late afternoon, although at times they hovered at mid-depths throughout the day. They evidently moved to the surface in large numbers at night, judging from the feeding activity of birds in the early morning hours. Pelicans do not appear to feed on red crabs, and when they are among a group of diving and working birds their feed would invariably be small baitfish rather than crabs. Boyd (1967), however, included pelicans among the predators of red crabs.

The cruise experience confirmed as well as contradicted published accounts regarding the crabs. The size of the crabs corresponded closely to that given by Boyd (1967). Samples taken from various localities showed remarkably little difference in size, ranging from 0.59 to 1.02 inches and averaging 0.85 inches in carapace length at all areas fished. Samples from Bahia Magdalena taken at 0900, 1500, and 1800 hours showed no difference in range or average size.

At Bahia Magdalena, some indications of diurnal migration were noted, but even during daylight hours the crabs did not settle directly on the bottom (Fig. 10A). Rather, they typically were distributed from the bottom

Table 6.—Summary of fishing activity aboard *Lady Olga*, 16-24 April 1973.

Date	Locality	Bottom depth (fm)	Surface temp (F)	No of tows	Avg duration of tows (min)	Avg catch per tow (lb)	Total catch (lb)
4/16	Pta. Abreojos	10-15	59	4	59	138	550
4/17	Bahia San Juanico	10-15	62	6	50	392	2,350
4/18	Bahia San Juanico	7-13	62	2	62	825	1,650
4/19	Bahia San Juanico	5-10	62	1	50	100	100
4/19	Bahia Santa Maria	20-22	62	1	32	100	100
4/20	Bahia Magdalena	5-15	64	4	13	1,500	6,000
4/21	Bahia Magdalena	5-15	64	9	37	833	7,500
4/22	Bahia Magdalena	5-15	64	6	31	1,350	8,100
4/23	Bahia Magdalena	10-15	64	4	38	3,150	12,600
4/24	Bahia Magdalena	12-15	64	2	30	1,825	3,650
				39	40	1,092	42,600

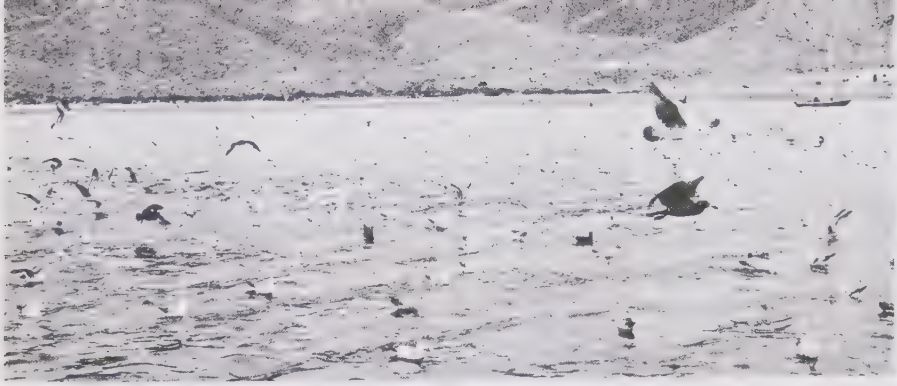


Figure 11.—Birds sitting on and flying low over the water, feeding on red crabs at the surface. Most of the birds are juveniles.

to about midwater. Whether or not the crabs near bottom were sitting on each other is not known.

Boyd (1962) found that wave and wind action was responsible for strandings of red crabs on beaches. We found, however, that crabs were being stranded daily in a quiet cove where the wind and waves moved offshore rather than toward the beach. It seemed that the crabs were being stranded by the receding tide rather than by wave action. Cadieux (1973), on the other hand, observed many crabs actually walking out of the water to die on the beach. Hundreds of birds lined the beach where the crabs were washed ashore (Fig. 3), but they did not appear to feed on crabs on the beach. The birds occasionally took flight and picked up dead crabs that were awash in shallow water and returned to the beach to eat them. We noticed also that most, if not all, of these birds were adults, while most of the birds feeding on live crabs away from the shore (Fig. 11), had the mottled markings of juvenile birds.

Our fishing was confined to shallow, protected bays because of high seas. We found evidence of large concentrations of crabs in deeper offshore waters, however. About 15 miles north of Cabo San Lazaro (lat 24°48′N, long 110°18′W) during daylight, the Fathometer indicated large numbers of crabs in the top 10 fathoms. At the surface, narrow but long windrows of crabs were oriented in line with the strong northwest wind.

At Thetis Bank about 18 miles northwest of Cabo San Lazaro, we found crabs near the bottom in large numbers (Fig. 8). Fish caught there had stomachs full of red crabs, and many crabs were seen near the surface. Somewhat to the north of Thetis Bank in deep water at night, Fathometer traces of crabs were solid from the surface to a depth of 30 fathoms.

FUTURE OF THE FISHERY

Development of a new fishery is always difficult. Even if the availability of a resource is known, studies are still necessary on all aspects from fishing to marketing. In the case of red crabs, the task is even more difficult because conventional uses for crustaceans do not apply, and new uses have to be developed. The future of the fishery lies in the success or failure of these new uses.

Certainly one of the more important areas of research is the value of red crabs as a coloring agent for pen-reared salmon. Current research being conducted by NMFS in Seattle on the optimum feeding rates and times will provide data necessary for evaluation and economic comparison with other sources of carotenoid pigments. Three of the five commercial firms in the United States now rearing salmon have enough supplies of red crabs to also undertake such feeding experiments. If results are favorable, red crabs may become an important component of the salmon's diet.

Along with this research other work related to use of red crabs as salmon feed is being done at NMFS Pacific Fishery Products Technology Center at Seattle. One aspect is to attempt to stabilize the carotenoid pigments of red crabs so that they can be included in dry pellets, which are cheaper to produce than other forms of salmon feed. Under normal heat-drying processes used in making dry pellets, the carotenoid pigments of red crabs may lose their effectiveness. Another aspect is directed toward separating the crabs into two fractions, one with high protein and carotenoid pigments (for salmon feed), and another with low protein and high chitin for other uses (Spinelli, Lehman, and Wieg, in press).

Even if red crabs become an integral part of the diet of pen-reared salmon, the total tonnage needed for this purpose will only be about a hundred tons per year. Other uses will have to be developed in order to sustain a fishery for crabs. The use of the flesh-coloring property can be carried over to other fishes and animals where external rather than internal coloration is desired, for example in aquarium fishes. Research is needed, however, to determine the effects of red crabs in the diets of various species of animals. In rainbow trout, at least, red crabs produce brilliant external coloration as well as pink flesh (Loren Donaldson, University of Washington, pers. comm.). If the same results can be achieved with aquarium fishes, and if the feed can be packaged in a convenient form this might become a major use for the crabs.

The chitin found in red crab shells could possibly form the basis of a major industry. Chitin is the structural material that holds together the shells of crustaceans. Presently a pilot plant near Seattle, Wash. is testing the feasibility of extracting chitin from shells of crustaceans. Chitin is similar in nature to cellulose and can be used in place of cellulose in some products. From chitin also, a material called chitosan can be derived, opening up a surprising variety of uses in papermaking, food, pharmaceuticals, sewage treatment, and many other applications (Pacific Northwest Sea, 1973).

Inclusion of red crab in pet food is still undergoing research. If results are favorable, the crab market could increase severalfold and the fishery would be assured a sound base. Of course, with the cost of fish meal rising dramatically, the possibility exists of using red crabs directly as fish meal despite their relatively low protein and high fiber content. Recent studies show that high-quality meal can be manufactured from crustaceans (Meyers and Rutledge, 1971).

Another possible use for the shell of red crabs is in horticulture. Dried and pulverized crab shells, when added to acid soil, would act to neutralize the soil and would also be useful as a slow releaser of nitrogen (Maynard Steinberg, NMFS, Pacific Fishery Products Technology Center, Seattle, pers. comm.).

Several possibilities exist for using the crabs as food. For example, the meat can be separated from the shell mechanically and used in soups or minced crab patties. The entire animal could also be used to prepare a concentrated protein paste (Minoru Okada, Tokai Fisheries Research Laboratory, Tokyo, Japan, pers. comm.). Alternately, red crabs can be ground and used as flavoring in fish cake products; experiments along this line have proved promising. Still another way of using red crabs as a flavoring agent is to dry and pulverize the whole crab.

Ultimately, the future of the pelagic red crab fishery will depend on the ex-vessel price of the crabs. Obviously, a lower price will attract more users and make feasible the use of all or parts of the crabs in a variety of products. In order for fishermen to operate at a low price, the efficiency of operations must be improved aboard the vessels. Our experience shows that improvements are needed mainly in the handling of the crabs once they are caught. Presently, catching the crabs is relatively efficient compared to handling and storing. Both midwater and bottom trawl are effective gear.

Probably the most efficient means of processing red crabs aboard a vessel would be to grind them. With the aid of suitable machinery, the ground crabs can be fed into bags and sealed automatically. Grinding would not only make handling easier, but would also decrease the volume of the crabs and hence increase the carrying capacity of a vessel. Further, refrigeration and ultimate freezing would be faster because air spaces would be eliminated. A disadvantage of grinding is that it may be impossible to make some contemplated products with ground crabs.

Prospects look good for the development of the red crab fishery. Ongoing studies are showing promising results, and it is likely that several experimental products will prove practicable. It should be pointed out, however, that although red crabs can be caught in international waters, the center of distribution lies well within Mexico's territorial limits. Thus, users here may have to depend on obtaining supplies from Mexico. For the present, Mexico is allowing some American fishing activity for the purpose of providing a supply of crabs to facilitate experimentation with various products and encourage development of fishing and handling methods. At the same time, Mexican scientists are studying the distribution and abundance of pelagic red crabs and are actively researching potential uses.

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CHEMICAL SIGNALS IN THE SEA: MARINE ALLELOCHEMICS AND EVOLUTION[1]

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ABSTRACT

Observations in chemical ecology suggest the coevolution of "natural products" of plants and the chemoreceptors of herbivorous insects. We have reviewed evidence which suggests that this coevolution extends back to the primordial protistans. Thus, the evolutionary pressure for the development of a chemosensory capability probably derived from the presence of metabolic products in the milieu. These products are considered to have been both cues to the location of prey and "membrane irritants" evolved in the initial phase of chemical protection. Sometime later this chemosensory capability provided several functions in the evolution of metazoans, i.e. the precursors of developmental signals, hormone function, and synaptic transmission.

We consider that most of the extant "natural products" of plants and marine invertebrates are protective allomones. A feature of allomone function that has been termed "antifeedant" or "feeding inhibitor" may represent the "cryptic odors" of Haldane. We provide evidence that the naphthoquinones with a juglone or naphthazarin structure have this activity. Octopus ink has a "cryptic odor" effect on moray eels. Marine Crustacea have, however, evolved an ability to perceive the orthoquinone precursors of the ink, a warning signal.

Evidence for an array of sex pheromones in a crab and a cycloid swimming pattern in a copepod that may enable it to follow a chemical gradient indicate the complexity of behavioral responses to chemical cues.

The earliest form of interaction between organisms was probably by means of chemical agents. This interaction involved both conflict and cooperation and its existence implies detection of these agents. Haldane (1955) first suggested that chemical communication is the most primitive form of communication, orginating with primordial unicellular organisms. He reasons that this primordial protistan communication was a necessary prelude to the evolution of metazoans and thus is a lineal predecessor of synaptic transmission and hormone reception. This early chemical communication may have evolved as an accessory to the active transport mechanism of the cell membrane or as a "membrane sensitivity" to metabolic by-products (Wynne-Edwards, 1962). That a more detailed understanding of transducer physiology is central to further advances in neurobiology has been emphasized by Delbrück (1970). He considers the stimulus-response system represented by chemoreception or synaptic transmission to be homologous.

We wish to examine some of the recent concepts of chemical ecology and to present examples from the marine environment. Studies of chemoreception are providing evidence for the pervasive function of chemical signals in the environment. The "membrane sensitivity" concept of Wynne-Edwards may provide a clue to both the initial evolution of a transducer function and the continuing evolution of receptor sites of greater diversity and specificity. It is evident that this diversity has resulted from a continual interplay of chemical countermeasures and the development of neurosensory and behavioral adaptations to these agents.

ALLELOCHEMICS

At all levels of life we are finding examples of attack, defense, and behavioral response

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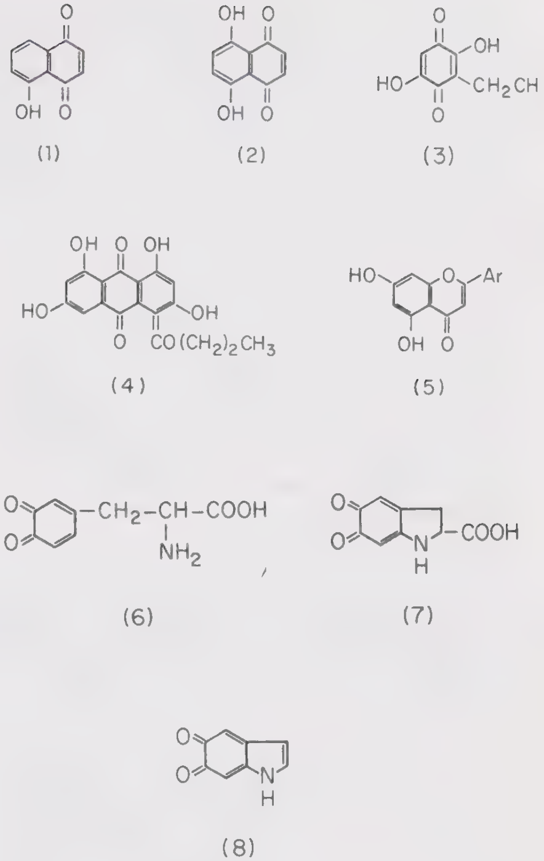
based on chemical agents. These interactions and the characterization of the chemical agents involved are the subject of the newly developing field of chemical ecology (Sondheimer and Simeone, 1970). Chemicals that are syntheized and released by one individual of a species to alter the behavior of other members of the species are termed pheromones. These signals range in their function from trail markers and territorial markers through alarm and defense signals to those which control caste structure in social insects and the sex pheromones that are calling signals and aphrodisiacs. Chemicals also have a wide range of interspecific interactions. A substance produced by one organism may influence the behavior of members of other species. A flower scent that enhances pollination is a well-known example. This field of chemical ecology has been termed allelochemics, and the chemical agents have been subdivided on the basis of function into allomones, which give adaptive advantage to the producing organism, and kairomones, which give adaptive advantage to the receiving organism (Whittaker and Feeny, 1971). The allomones include the repellents produced by many plants and animals, suppressants which inhibit competitors (e.g., fungal antibiotics), venoms, inductants (e.g., gall producing agents), and attractants (e.g., chemical lures). The kairomones include attractants (e.g., the scent of a prey), inductants (e.g., the factor that stimulates hyphal loop development in nematode-trapping fungi), danger signals (e.g., predator scents, secondary plant substances indicating toxicity), and stimulants (e.g., hormones that induce growth in the receiving organism).

The diverse natural products, coumarins, quinones, flavonoids, acetylenes, terpenoids, saponins, cardiac glycosides, alkaloids, thiols, and cyanogenic glycosides, which were long considered metabolic waste products, are now recognized to be allelochemic agents. Examination of the function of these natural products provides some insight into their evolution. Some of these compounds are toxic, some are chemical lures, others inhibit the growth of competitive plant species, but the bulk of these compounds probably function as "feeding inhibitors" of herbivores (Gilbert, Baker, and Norris, 1967; Munakata, 1970). The coevolution of butterflies and plants is considered by Ehrlich and Raven (1964). They emphasize the role of reciprocal selective responses during this evolution and conclude that "the plant-herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity." The "accidental" evolution of a metabolic sequence resulting in the production of a noxious substance by a plant provided a selective survival advantage in the clone carrying this capability. Decreased predation by herbivores on those individuals containing the highest concentrations of the new substance resulted in genetic selection for increased synthesis and storage of the noxious substance. Such "protected" species experience an explosive increase because of their protection from contemporary phytophagous organisms. The first evolutionary response of the herbivores must have been the development of the capability to detect the compound, i.e. sensitive external chemoreceptors. Later evolutionary events led to the development in some individuals of a tolerance for the noxious substance. The herbivores which developed this tolerance then had access to a large food supply for which there was no competition. The ability to detect the substance then had an altered function, the feeding inhibitor was now a feeding stimulant. The present evidence of the repeated occurrence of this cycle is the existence of tightly coupled herbivorous insects and their host plants, presumably arising through coadaptation.

In 1955 Haldane, in a consideration of chemical communication and visual signals, wondered if cryptic odors had ever evolved. While most of the feeding inhibitors that have evolved are probably irritants, many may be cryptic odors. It is likely that the two activities may only differ in the membrane affected. The term irritant implies membranic sensitivity and, of those membranes of an organism in immediate contact with the environment, the chemosensory membranes are likely the most sensitive to chemical irritation. In an environment in which a major fraction of the information flow is chemical, any agent capable of disrupting the chemosensory organs of a predator would provide an ideal mechanism for "hiding" from that predator. Cryptic odors may be either "negative odors" altering, for protracted periods, the membrane potential of the dendrites and blocking their normal generator potential, or they may be the chemical equivalent of a "white noise," producing an "uncoded" array of spikes in the chemosensory neurons.

The best description of behavior suggesting a "cryptic odor" in the marine environment is that given by MacGinitie and MacGinitie (1968). The ink of an octopus is considered a "smoke screen"; however, it can also affect the olfactory sense. The MacGinities observed that after a moray eel swam through the ink cloud of an octopus it could no longer "recognize" an octopus. The moray eel apparently requires both visual and olfactory input for this recognition. They state, "We were surprised to find that the real effect of the ink of an octopus is to paralyze the olfactory sense of its enemies." The melanin of the ink is a polymer of oxidized L-DOPA. The polymerization proceeds through three orthoquinones, dopaquinone (6, Figure 1), dopachrome (7), and indole-5, 6-quinone (8). In the biosynthesis of melanin, this oxidation is catalyzed by polyphenyl oxidases; however, heavy metal ions can also catalyze the oxidation, and it can be readily demonstrated that the trace of heavy metal ions in seawater will rapidly convert L-DOPA to melanin. The octopus ink loses its potency with time, a factor that would indicate that the biological activity of the ink is due to the presence of the unstable monomer orthoquinones in the fresh ink (Kittredge, Takahashi, and Lindsey, unpublished data).

The observation of Gilbert et al. (1967) that juglone (5-hydroxy-1,4-naphthoquinone) (1, Figure 1) is a deterrent to feeding by the bark beetle, *Scolytus multistriatus*, suggested a similar function for the polyhydroxynaphthoquinones occurring in the echinoderms. These spinochromes are all derivatives of juglone (1) or naphthazarin (2). They occur as soluble salts in the tissues and may be present in considerable amounts in the larvae. They also occur as insoluble calcium salts in the spines and tests (Thompson, 1971). The echinoids have received the closest attention, but P. J. Scheuer and his group have demonstrated the presence of these compounds in the other four classes of this phylum—the holothurians, asteroids, ophiuroids, and crinoids (Singh, Moore, and Scheuer, 1967). They also demonstrated the presence of a substituted 2,5-benzoquinone (3) in the genus *Echinothrix* (Moore, Singh, and Scheuer, 1966). The crinoids are interesting in that they contain primarily a series of polyhydroxyanthroquinones (e.g., rhodocomatulin, 4) (Sutherland and Wells, 1967; Powell, Sutherland, and Wells, 1967; Powell and Sutherland, 1967; Matsuno et al., 1972; Erdman and Thomson, 1972).



(1) (2) (3) (4) (5) (6) (7) (8)

FIGURE 1.—Structures of compounds typical of those which may function as "cryptic odors." (1) juglone, (2) naphthazarin, (3) 2, 5-dihydroxy-3- ethylbenzoquinone, (4) rhodocomatulin, (5) flavone, (6) dopaquinone, (7) dopachrome, (8) indole-5,6-quinone.

Utilizing the "feeding response" of the lined shore crab, *Pachygrapsus crassipes*, which consists of a rapid lateral movement of the mouthparts when presented with a feeding stimulus, we have bioassayed the "feeding inhibitor" activity of juglone and eight representative spinochromes. The "feeding stimulus" was a 20-μl aliquot of a 3-mM solution of taurine in seawater administered from a repeating syringe close to one of the antennules of the crab. Initially the crabs were immersed in a 1-μM solution of the naphthoquinone and tested for a feeding response. Five experimental and one control crab were utilized for each compound. No feeding responses were observed in any of the test crabs while all of the controls were positive. A second series of bioassays was designed to determine the onset of inhibition. The crabs were placed in seawater and stimulated with 20 μl aliquots of a solution of 3 mM taurine and 1 μM quinone. The stimulus was administered at 2 sec intervals to alternate antennules. Inhibition of the "feeding response" was observed at approximately 10 sec. The naphthazarin derivatives were apparently more potent than the juglone derivatives. We interpret these results as indicative of a "cryptic odor" function; the crabs cannot detect the feeding stimulant after a brief exposure to the quinone.

Many higher plants contain juglone or other hydroxynaphthoquinones or benzoquinones. These compounds also occur in fungi, lichens, pholangids, millipedes, and insects. 1,4-benzoquinones are the most common ingredient of insect defensive secretions and the 2,5-substituted 1,4-benzoquinones are characteristic of fungi. A similar "cryptic odor" function may be predicted for these compounds.

Norris (1969) compared the feeding deterrent activity of a number of substituted naphthoquinones. Juglone (1) and naphthazarin (2) were the most potent inhibitors. The apparent effectiveness of the hydroxy groups in the 5- or 5,8-positions in these naphthoquinones suggests an examination of the function of the major group of secondary plant metabolites, the flavones (5) (Harborne, 1972) which have a marked structural similarity.

Whittaker and Feeny (1971) predict "that research into the relations of multicellular marine algae and their consumers will reveal chemical defenses and responses paralleling those of higher plants and animals on land." The most likely candidates to fulfill this prediction are the highly halogenated hydrocarbons that are synthesized by algae and stored in the tissues of the herbivorous gastropod, *Aplysia californica* (Faulkner and Stallard, 1973; Faulkner et al., 1973). We would add to the prediction of Whittaker and Feeny that research into the relations of many marine invertebrates and their predators may reveal allomones. Some of the "natural products" of marine invertebrates that have been recently characterized and that may have this function are the halogenated antibiotics that have been isolated from sponges (Sharma, Vig, and Burkholder, 1970; Fattorusso, Minale, and Sodano, 1972; Moody et al., 1972; Anderson and Faulkner, 1973). Steroid saponins that are toxicants or irritants have been characterized from holothuroids and starfish (Yasumoto, Nakamura, and Hashimoto, 1967; Tursch et al., 1967; Roller et al., 1969; Tursch, Cloetens, and Djerassi, 1970; Turner, Smith, and Mackie, 1971).

We recall a simple demonstration by the late C. F. A. Pantin of the sensitive chemosensory capability of sea anemones for saponin. The nematocysts of sea anemones require both a mechanical and a chemical stimulus for discharge. One can brush the surface of a sea anemone's tentacles with a clean glass rod without effecting any discharges. If, however the glass rod is first dipped into a dilute saponin solution, a massive discharge is effected.

An observation by Clark (1921) suggests the existence of allomones in crinoids. He discusses the avoidance of comatulid crinoids by fish and suggests the activity of glands at the base of the tentacles. The comatulids are unique in containing both polyhydroxyanthroquinones and aromatic polyketides (Kent, Smith, and Sutherland, 1970; Smith and Sutherland, 1971).

MARINE KAIROMONES

As in the terrestrial environment, invertebrates utilize chemical cues to locate hosts or to warn of predators. Davenport (1966) demonstrated the response of commensal polynoid polychaetes to a "host factor" in the water draining from tanks containing the host species of starfish. In an electrophysiological analysis of the antennular chemoreceptors of two commensal shrimps, Ache and Case (1969) demonstrated the specificity of the response to "host water" from the specific hosts, *Haliotis* spp. and *Strongylocentrotus* spp.

Predatory starfish induce an escape response in a variety of molluscs (Feder, 1967), and these behavioral responses probably effectively reduce the predation on these species that can detect the predator (Feder, 1963). The active materials in extracts of the starfish *Marthasteria glacialis* and *Asterias rubens* which induce the escape response have been shown to be steroid saponins (Mackie, Lasker, and Grant, 1968).

The threshold for response by the snail, *Buccinum undatum* is $0.2-0.4 \times 10^{-9}$ M (Mackie, 1970), and the structure of these steroid glycosides has been determined (Turner et al., 1971).

A behavioral bioassay of one of the orthoquinones derived from L-DOPA, dopachrome, utilizing the feeding response of the lined shore crab *Pachygrapsus crassipes* indicated that this quinone might also be a "cryptic odor." Electrophysiological studies, however, demonstrated that these results were misleading. Utilizing a preparation of the dactyl chemoreceptors of the spiny lobster *Panulirus interruptus,* we detected chemoreceptors for this quinone that were about a hundred times as sensitive as the general amino acid receptors in this preparation (Figure 2). While we have not explored the range of specificity of these receptors, the results suggest that these crustaceans, the natural prey of the octopus, have evolved a mechanism for detecting the presence of the predator. Our results with the bioassay likely reflect a priority of responses to the two chemical stimuli (Kittredge, Takahashi, and Lindsey, unpublished data).

PHEROMONES

Unicellular chemical communication, analogous to Haldane's primordial protistan communication, is evident in the conjugation of ciliates. The microconjugant of a peritrichous ciliate, which is free swimming, can identify the macroconjugant, which is sessile, by chemicals released by the latter. Although evidence for

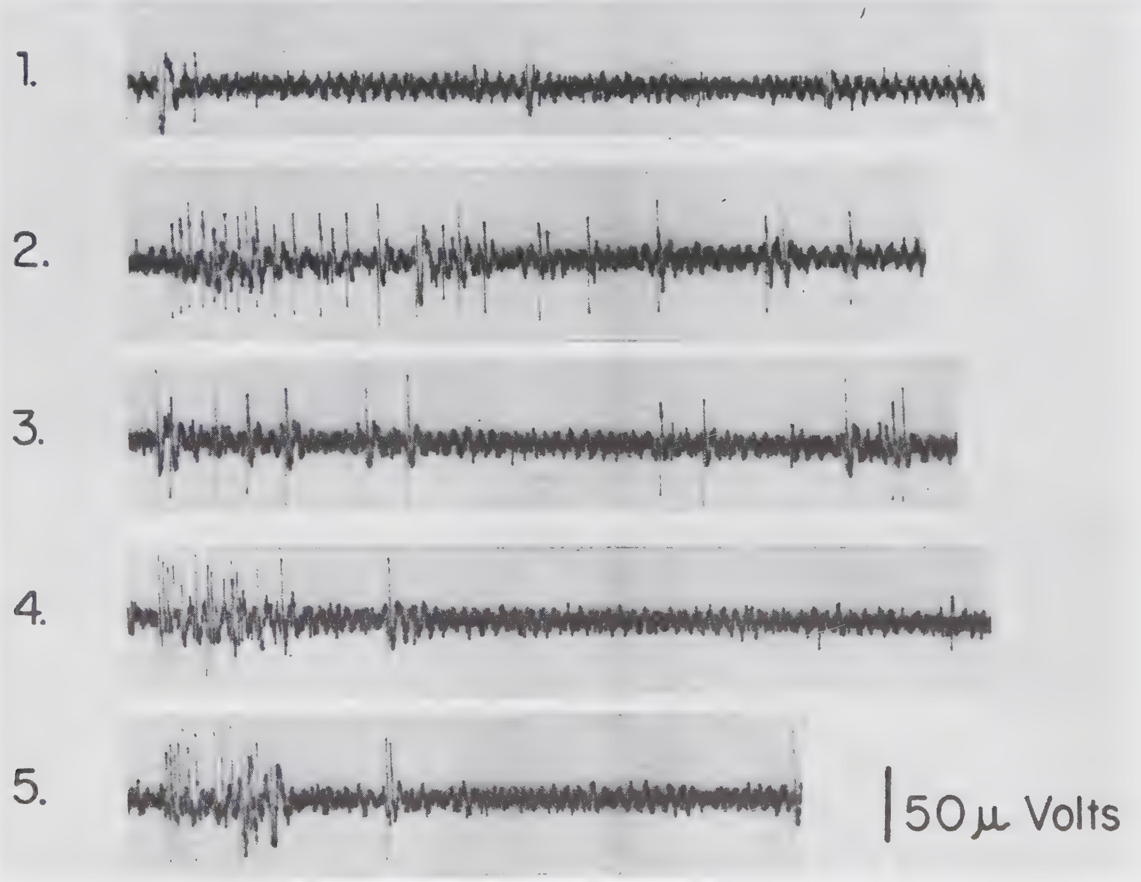


FIGURE 2.—Electrophysiological recordings from the dactyl chemoreceptors of a spiny lobster, *Panulirus interruptus.* (1) Seawater blank, (2) 10^{-5} M dopachrome in seawater, (3) Persisting spikes in dopachrome receptors (continuation of 2), (4) 10^{-3} M taurine in seawater, (5) 10^{-3} M taurine after dopachrome and a seawater wash.

the presence of a large number of agents chemotropic for male gametes exists (Machlis and Rawitscher-Kunkel, 1963), only two have been chemically characterized. Sirenin, the active compound produced by the female gametes of the water mold *Allomyces*, has been isolated and characterized as an oxygenated sesquiterpene (Machlis et al., 1966), and its structure has been uniquely established (Machlis, Nutting, and Rapoport, 1968). It is active in attracting male gametes at 10^{-10}M. The corresponding work from the marine field resulted in the characterization of the active substance released by the female gametes of the brown alga *Ectocarpus siliculosus* as allo-cis-1-(cycloheptadien -2′, 5′-yl)-butene-l (Müller et al., 1971). The receptor sites on the male algal gametes evidence a low level of specificity. Many lower hydrocarbons, esters, alcohols, and aldehydes, at higher concentrations, will mimic the natural compounds in attracting male gametes (Cook, Elvidge, and Bentley, 1951; Müller, 1968; Hlubucek et al., 1970).

Though many efforts to demonstrate a chemotactic response by mammalian sperm to substances from eggs have yielded negative results, such attraction does occur in marine forms. Sperm of the thecate hydroids *Campanularia flexuosa* and *C. calceolifera* respond to a substance issuing from the aperture of the female gonangium. The response is species specific (Miller, 1966). Observations by Dan (1950) suggest the activity of a similar substance from the eggs of the medusa *Spirocodon saltatrix* on the sperm of this species. The first examples of sperm chemotaxis in vertebrates are described in papers on fertilization in the herring *Clupea* by Yanagimachi (1957) and in the bitterling *Acheilognathus* by Suzuki (1961).

The attraction of the amoeboid form of the slime mold *Dictyostelium discoideum* during the aggregation phase which results in the formation of a multicellular "slug" represents the best studied protistan communication. The attractant is cyclic adenosine monophosphate (Konijn et al., 1968; Barkley, 1969). Pulses of cyclic AMP radiate out through the soil moisture at 5 min intervals from the center of a growing aggregation. The gradient and the pulse nature of the signal are maintained by each inward streaming amoeba. Each amoeba secretes a phosphodiesterase to break down the cyclic AMP and, on sensing a pulse of cyclic AMP, emits its own pulse of cyclic AMP about 15 sec after receiving a signal (Cohen and Robertson, 1971; Robertson, Drage, and Cohen, 1972). Bonner (1969) has indicated the likely course of the evolution of this communication in the social slime molds. Soil bacteria, the food of the solitary predecessors of the slime mold amoeba, secrete cyclic AMP. It is reasonable to assume that a mechanism which initially increased the feeding success of these amoebas developed, due to selective pressure, the requisite high sensitivity of response to a chemical signal necessary for aggregation. This capacity then facilitated the evolution of the social species. This is very close to Haldane's premise of the evolution of chemical communication prior to the evolution of metazoans. In further support of Haldane's premise of the lineage of hormones, after aggregation is complete the "metazoan" slug phase migrates to the soil surface and then certain cells differentiate into stalk cells which will eventually support the spore head. Cyclic AMP is apparently the chemical signal for the developmental differentiation of some cells into stalk cells (Bonner, 1970).

The recent rapid growth of our understanding of pheromone communication in insects was founded on half a century of acute biological observations which implicated the existence of chemical messengers. The isolation and chemical characterizations of a growing number of pheromones, and the concomitant behavioral studies, have provided the basis for our appreciation of the role of chemical communication in the life cycle of many species. Among the many recent reviews are those of Beroza (1970) and Jacobson (1972). Electrophysiological investigations of chemoreception in insects have demonstrated that the receptor cells may be divided into two groups, either "specialists" or "generalists" (Yamada, 1970). Among the "specialists" are the pheromone receptors and the receptors for specific secondary plant substances that act as phagostimulants (Schoonhoven, 1968). While remarkable success has been achieved in recording the response of single receptor cells as well as the summed receptor potential of all the antennal chemoreceptors (electroantennogram) these workers have had to contend with a technical problem inherent in studies with this material. Evaluation of the response of a chemosensory organ or a single cell is difficult when the stimulant must be presented in the gas phase. Each species of stimulant molecule must partition between the gas phase and an aqueous film. The active concentration at the receptor membrane is unknown. A study of the physiology of pheromone reception by aquatic organisms would avoid this limitation.

A survey of the literature reveals that, as in the field of entomology, there exists a broad basis of behavioral observations suggesting the role of chemical communication in the aquatic environment. These studies suggest that marine invertebrates are primarily dependent on chemoreception for information from their environment. The input is composed of a broad spectrum of chemical messages ranging from species specific pheromones eliciting stereospecific responses, e.g., mating behavior, epidemic spawning, aggregation, or alarm behavior, through those kairomones triggering metamorphosis or migration to the cues indicating the proximity of predators or prey.

The closest parallel to insect pheromone communication observed in marine organisms are the sex pheromones of marine crustacea. The first experimental demonstration of "chemical recognition" by marine crustacea is the description of the behavior of male copepods *(Labidocera aestiva)* by Parker (1902). In a series of elegantly simple experiments he demonstrated that "they [the females] probably give rise to some substance that serves as a scent for the males; in other words, the males are probably positively chemotropic toward the females." Moreover Parker noted that "they [the males] seldom pass near the tube without some characteristic reaction. Usually they made one or two quick circles as they swam by, or even a somersault-like motion; these were observed fifteen times when the females were in the tube, never when they were not." Lillelund and Lasker (1971) observed similar swimming behavior in male *Labidocera jollae.* Although *L. jollae* females swim in a seemingly random pattern with only occasionally looped excursions, the males frequently vary their random course of a few seconds duration by swimming in circles, covering a small area intensively. Of greater interest was the observation that rather than circles, the path of the males often resembled a curtate cycloid. The males occasionally progressed for several centimeters in this curtate cycloid path (Figure 3). These observations, although obtained during feeding studies, suggest an important aspect of the physiology of pheromone response in small crustacea—the mechanism of sensing a chemical gradient. Crisp and Meadows (1962) have stated that, because of the small distance between the chemosensory organs of barnacle cyprid larvae, these larvae cannot detect a chemical gradient and thus

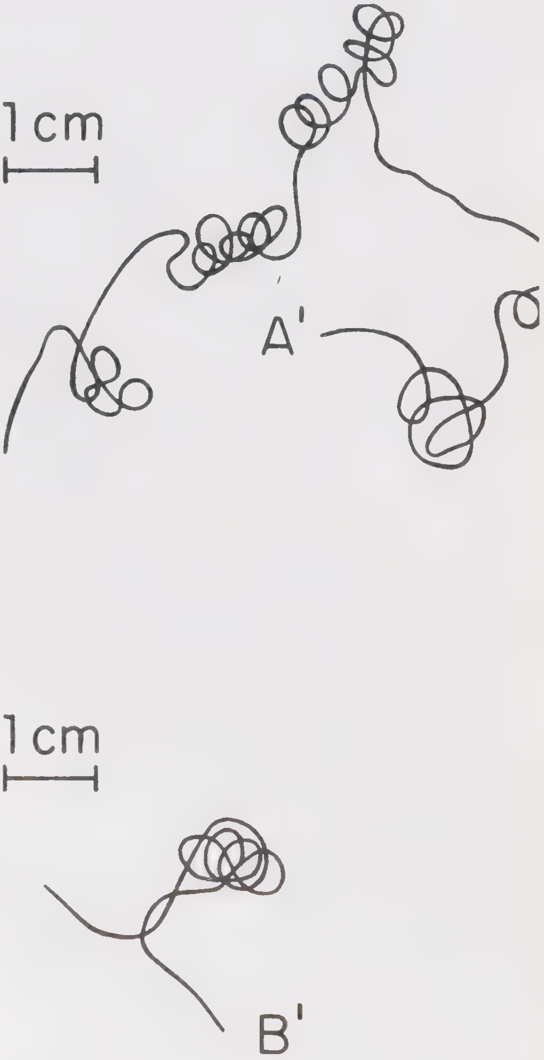


FIGURE 3.—Swimming behavior of a male copepod *Labidocera jollae.* A′ and B′ mark the termini of the tracings. The upper trace shows both an occasional circular swimming course, progression in a curtate cycloid course and "doubling back." The lower trace is an extreme example of the "doubling back" behavior.

cannot exhibit chemotactic behavior. This reasoning has been applied to all small marine crustacea including copepods. From the above observations it is apparent that the reasoning of Crisp and Meadows is invalid for *Labidocera* and probably for other small crustacea. The critical dimension is the diameter of the circular course, not the dimensions of the organism. A circular swimming pattern in a concentration gradient of a stimulant would result in a sinusoidal variation in the signal intensity. Alteration of the radius of curvature of the swimming course in response to this sinusoidal input would result in cycloidal progression in the gradient. It appears from the observations of the behavior of male *L. jollae* in the feeding experiment that a threshold level of stimulant will trigger a circular swimming pattern, if this circular course results in the detection of a gradient, the circular course will become a curtate cycloid with the ratio of the major to the minor radius being a function of the intensity of the gradient. A frequent observation is a doubling back. If several progressions of the cycloid result in loss of the gradient signal (as must frequently occur in a medium in which the dimensions of the turbulent flow are of the same scale as the swimming pattern), the swimming plots indicate that the male *Labidocera* can effectively loop back through the area where the signal was initially detected (Figure 3). These observations indicate some power of spatial orientation and short term memory in *Labidocera.*

In crabs the male is attracted to the premolt female. During this attraction phase he may display a stance characterized by standing on the tips of his dactyls and elevating his body. He will seize the premolt female and place her below his body. He will protect her during the vulnerable molting period and they copulate immediately after molting. Ryan (1966) demonstrated pheromone communication in this interaction. Water from a tank containing a premolt female *Portunus sanguinolentus*, when added to a tank containing a male of this species, elicited the premolt stance. Evidence that the pheromone is released from the antennule glands was provided by sealing these glands and noting the absence of the stimulating factor.

We have examined this pheromone communication in the lined shore crab, *Pachygrapsus crassipes.* We isolated an active substance and found that it behaved chromatographically like the molting hormone, crustecdysone. Pure crustecdysone is active in stimulating all of the precopulatory behavior of male lined shore crabs from an early search behavior through the display stance to seizing the female. The threshold for stimulating the stance is 10^{-13} M (Kittredge, Terry, and Takahashi, 1971). Confirmation of the identification has been obtained by injecting tritiated crustecdysone into intermolt female Dungeness crabs *(Cancer magister)* and detecting its release as the females entered premolt. Recently we have detected the presence of two additional pheromones released by the female lined shore crabs. Compound A is released in addition to crustecdysone prior to molt. After molting compound A is no longer released into the water, but, if the female is held in isolation from male crabs, a second compound, B, is released. It is likely that the postmolt female has a different message to transmit.

Evolutionary biologists concerned with the inception of pheromone communication have long been puzzled by a dilemma. This chemical communication implies two new capabilities, that to synthesize a messenger compound and the ability to receive the message and translate it into a behavioral response. The improbability of the simultaneous occurrence of these two *de novo* events suggests a stepwise sequence. The observation that the molting hormone of crustacea can function as a sex pheromone indicates that the primordial Arthropoda, through an evolutionary sequence that resulted in structuring the receptor site for the hormones on chemosensory membranes, were able to initiate pheromonal communication (Kittredge and Takahashi, 1972).

SUMMARY

Evidence from the literature supports Haldane's premise that chemical communication is the most primitive form of communication and thus the lineal predecessor of synaptic transmission and hormone function. Transducers of environmental chemical information have likely evolved in response to the metabolic products released by their prey and by competitive organisms. This coevolution of "natural products" and the respective transducers has existed from the earliest metabolic product that happened to be a membrane irritant to the

present. We thus consider it likely that most of the "natural products," not only of terrestrial plants, but also of marine plants and invertebrates, function as allomones, kairomones, or pheromones. Faulkner and Anderson (In press) have provided a review of the chemistry of the "natural products" of marine organisms.

Conceptually, in such a "chemical environment" the most effective protection from a predator would be a "cryptic odor," an irritant that disrupts chemoreception. These cryptic odors may be released into the environment, as is the active component of octopus ink, they may exist in the epidermal tissues or glands where they would function at the inception of attack, or they may be contained in the eggs or larvae. Most sessile marine invertebrates reproduce by epidemic spawning, the simultaneous release of the gonadal products of an entire local population of a species. Most sessile marine invertebrates are also filter feeders. The prime advantage of epidemic spawning is the enhancement of fertilization. However, in the densely populated benthic environment, a heavy loss of eggs or larvae to filter feeders may occur. The presence of a "feeding inhibitor" in the eggs or larvae would reduce such losses. Reiswig (1970) reported that they observed epidemic spawning of the sponge *Neofibularia nolitangere* on a Jamaican reef. At the time they were measuring the water pumping rate of other sponges. When the epidemic spawning of *N. nolitangere* started, the pumping rate of the species under study, *Verongia* sp, abruptly decreased and remained negligible for 2 days. *N. nolitangere* is known to contain toxic substances.

The evidence for chemical cooperation, from gamones to sex pheromones, suggests a pattern of increasing complexity in the function of chemical cues. The behavioral response of even a "simple" crustacean to a chemical gradient appears to involve at least some short term "memory" or a type of "chemical-spatial" sense that we have not observed in such clear-cut form in any other organism.

The study of the chemical ecology of the marine environment is scarcely in its infancy. The chemical characterization of some of the intraspecific and interspecific messages in the sea and the physiology of their perception are challenges. Solutions to these paired problems will provide insights into the evolution of chemical transduction and perhaps expose a hierarchy of perception from membrane irritation to synaptic transmission.

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ACUTE TOXICITY OF TWENTY INSECTICIDES TO STRIPED BASS, *MORONE SAXATILIS*[1]

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The acute toxicity of twenty insecticides to juvenile striped bass was determined in saline water. All bioassays were four-day tests using proportional diluters as described by Mount and Brungs (1967).

Endrin, Endosulfan, DDT, and Dursban were the most toxic with Median Lethal Concentration (TL_{50}) values of less than 1 μg/l. Carbaryl and Abate were the least toxic with TL_{50} values over 1,000 μg/l. DDD, Heptachlor, Methoxychlor, Toxaphene, Aldrin, Lindane, Chlordane, Malathion, Parathion, Dieldrin, E.P.N., Fenthion, Dibrom, and Methyl Parathion were also tested and are listed in order of decreasing toxicity. Some advantages of intermittent versus static bioassay testing are discussed.

INTRODUCTION

The San Francisco Bay and Delta region represents the most important striped bass habitat on the west coast. It is also an area which receives large amounts of pesticides from drainage systems, primarily the Sacramento-San Joaquin Rivers. Insecticides in this study were selected because measurable quantities of 14 out of the 20 have been reported in the waters of this region (Water Resources Control Board, 1971). Earnest and Benville (1971) found DDT levels in bay water in Tiburon, California to vary from 3 to 21 ng/l during 1969. The other insecticides were selected because mosquito control districts and others indicated these compounds were either now being used or had potential for use in the bay-delta area.

This study was an effort to provide intermittent flow bioassay data for insecticides on striped bass. Information of this type is useful to screen out the more toxic compounds from those in use or being considered for application. The determination of acute toxicity is the first of a logical sequence of evaluative steps leading to the determination of chronic sub-lethal effects of compounds potentially harmful to aquatic organisms.

METHODS

Striped bass (14–83 mm SL, 0.06–4.8 g) were obtained from the fish diversion facility operated by the Bureau of Reclamation at the Tracy pumping plant, Tracy, California. Fish were transported in fresh water to our facility where they were acclimated over a 3 day period to bay water. The fish were further acclimated to test water conditions in

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[1] Accepted March, 1974

1,000 liter fiberglass tanks for at least 1 week before testing. Frozen brine shrimp were fed to the fish once daily to saturation.

The test water during the acclimation and test periods was filtered through a sand filter and salinity (Kahlsico salinity hydrometer), turbidity (Hach 2100 turbidimeter) and temperature were determined daily (Table 1).

TABLE 1—Toxicity of Insecticide to Striped Bass Listed in Descending Order.

Insecticide	Mean length (mm)	Mean weight (g)	Temp mean (C°)	Salinity mean (°/∞)	Turbidity mean (J.T.U.)	TL_{50} (95% C.I.) (ug/1)
Endrin	70	2.7	17±1*	28±2*	2	0.094 (0.045–0.19)
Endosulfan	33	0.3	16±1	30±1	1	0.1 (0.048–0.21)
DDT	70	2.7	17±1.5	28±1	2	0.53 (0.38–0.84)
Dursban	36	0.6	13±0.5	30±2	1	0.58 (0.35–0.97)
DDD	40	0.6	17±1	30±2	1	2.5 (1.6–4)
Heptachlor	33	0.5	13±1	28±1	1	3 (1–6)
Methoxychlor	70	2.9	15±0.5	28±	2	3.3 (2.1–5.1)
Toxaphene	60	2.3	17±1.5	30±2	1	4.4 (2–9)
Aldrin	70	4.3	13±1.5	28±2	2	7.2 (3.4–15.2)
Lindane	65	2.4	13±1	28±1	2	7.3 (4.5–11.9)
Chlordane	83	4.8	15±0.5	28±2	2	11.8 (5.7–24)
Malathion	34	0.4	13±1	30±1	1	14 (13–15)
Parathion	83	4.8	15±1	27±2	2	17.8 (4.8–65.7)
Dieldrin	78	4.3	14±0.5	28±2	3	19.7 (9.8–33.4)
E.P.N.	37	0.36	18±1.5	30±1	1	60 (25–150)
Fenthion	35	0.33	13±1	29±1	1	453 (216–955)
Dibrom	46	0.8	13±1	30±1	1	500 (100–2400)
Methyl Parathion	34	0.4	13±1	30±2	1	790 (170–1400)
Carbaryl	31	0.42	17±0.5	30±1	1	1000
Abate	14	0.6	13±1	30±1	1	1000

* Range

Water temperature was not controlled. Previous Winkler oxygen determinations with intermittent flow devices at this facility indicate that satisfactory oxygen levels are maintained with the biomass per tank used in these tests. We did not exceed 1g of fish per liter of water.

All bioassays were 4-day tests (96-hour) using proportional diluters as described by Mount and Brungs (1967). Stock solutions were prepared by dissolving the insecticides in ethanol. Fish were sorted for size and placed 10 per concentration in 80 liter aquaria. The fish were not fed the day before bioassays started or during bioassays. Mortalities were recorded daily, but only the 96-hour results are reported. The TL_{50} (tolerance limits for 50% of the test animals) values were determined by converting the data to logs and probits and calculating a linear regression according to a modification of the Litchfield and Wilcoxin (1949) method. Technical information on insecticides used is listed in Table 2.

RESULTS

Endrin, Endosulfan, DDT, and Dursban proved to be the most toxic to striped bass with TL_{50} values of less than 1 μg/l. Carbaryl and Abate were at the other end of the scale proving to be relatively nontoxic with TL_{50} values over 1000 μg/l (Table 1).

TABLE 2—Technical Insecticides Used for Striped Bass Bioassays

Pesticide		Activity* %	Source
Endrin	1,2,3,4,10,10-Hexachloro-6,7-epoxy 1,4,4a,5,6,7,8,8a-octahydro-1,4-*endo*-*endo*-5,8-dimethanonaphthalene	99	City Chemical Co.
Endosulfan	6,7,8,9,10,10-Hexachloro-1,5,5a,6,9,9a-hexahydro-6,9-methano-2,4,3-benzodioxathiepin-3-oxide		
DDT	1,1,1-Trichloro-2,2-bis(p-chlorophenyl) ethane	77.2	City Chemical Co.
Dursban	0,0 Diethyl-0-3,5,6-Trichloro-2-pyridyl phosphorothioate	99+	Dow Chemical Co.
DDD	1,1-Dichloro-2,2,-bis(p-chlorophenyl) ethane	99	City Chemical Co.
Heptachlor	1,4,5,6,7,8,8-Heptachloro-3a,4,7,7a-tetrahydro-4,7-methanoindene	99+	City Chemical Co.
Methoxychlor	1,1,1-Trichloro-2,2-bis-(p-methoxyphenyl) ethane	89.5	City Chemical Co.
Toxaphene	Chlorinated camphene with 67–69% chlorine	100	City Chemical Co.
Aldrin	1,2,3,4,10,10-Hexachloro-1,4,4a,5,8,8a-hexahydro-1,4-*endo exo*-5,8-dimethanonaphthalene	90	City Chemical Co.
Lindane	1,2,3,4,5,6-Hexachlorocyclohexane	100	City Chemical Co.
Chlordane	1,2,4,5,6,7,8,8-Octachloro-3a,4,7,7a-tetrahydro-4,7-methanoindan	60	City Chemical Co.
Malathion	5,(1,2-dicarbethoxyethyl)0.0-dimethyldithiophosphate ethyl phosphorodithioate	95	American Cyanamid Co.
Parathion	0,0-Diethyl-0-p-nitrophenyl phosphorothioate	--	American Cyanamid Co.
Dieldrin	1,2,3,4,10,10-Hexachlor-6,7-epoxy 1,4,4a,5,6,7,8,8a-octahydro-*endo-exo*-1,4:5,8-dimethanonapthalene	85	City Chemical Co.
E.P.N.	0-Ethyl-0-p-nitrophenyl phenylphosphonothioic acid	87.7	Du Pont
Fenthion	0,0-Dimethyl-0-[4-(methylthio)-m-tolyl] phosphorothioate	--	Chemagro Corporation
Dibrom	1,2-Dibromo-2,2-dichloroethyl dimethyl phosphate	90	Chevron Chemical Co.
Methyl Parathion	0.0-Diemthyl 0-p-nitrophenyl phosphorothioate	80	American Chemical Co.
Carbaryl	1-Naphtyl-N-methylcarbamate	98	Union Carbide
Abate	0,0,0′,0′-Tetramethyl 0,0′-thiodi-p-phenylene phosphorothioate	90	American Cyanide

* % of pure compound

DISCUSSION

It is realized that toxicity values may vary with fish size, temperature and salinity (Eisler 1970). Therefore, the order of descending toxicity presented in Table 1 may be altered with a more uniform size of fish and more controlled environmental conditions. The high variability in the results from certain tests was due to few data points being obtained. This would also affect the order of toxicity. Previous bioassay data in salt water to compare with this study is lacking. Wellborn (1971) reported 96-hour TL_{50} values for malathion and lindane on striped bass in fresh water under static conditions to be 0.24 and 0.40 mg/l, respectively. Our results were much lower, 0.015 and 0.007 mg/l, respectively. This can be explained in part due to the characteristics of static and intermittent bioassays.

All of our results were intermittent flow tests which are more meaningful than static tests. Under static conditions, oxygen and waste products can be stress-inducing factors (Lincer, Solon and Nair 1970). Also, pesticides may be absorbed by fish and glass resulting in higher TL_{50} values (unpublished data, Fish Pesticide Research Laboratory, Columbia, Mo.). Earnest and Benville (1972) found static bioassays generated higher TL_{50} values than intermittent flow tests with two species of fish and four organochlorine insecticides. Since many of the TL_{50} values in the past have been based on static tests, we feel more studies comparing static and intermittent flow tests are warranted. The actual toxicity of other pesticides currently being used in the San Francisco Bay Area may in fact be much higher than expected since toxicities were determined under static conditions.

ACKNOWLEDGMENTS

The laboratory research was conducted while the Bureau of Sportfisheries and Wildlife maintained a Fish Pesticide Research Laboratory at their Tiburon field station. Under terms of Administration Reorganization Plan No. 4, which became effective October 3, 1970, this field facility at Tiburon was transferred from the Department of Interior to the Department of Commerce. Data analysis and manuscript preparation were completed after the senior author's transfer to the National Marine Fisheries Service.

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LENGTH-WEIGHT RELATIONS FOR FIVE EASTERN TROPICAL ATLANTIC SCOMBRIDS

This paper presents an analysis of fork lengths and body weights of five species of scombrids measured from landings at several ports on the west coast of Africa during 1967 and 1968: yellowfin tuna, *Thunnus albacares*; skipjack tuna, *Katsuwonus pelamis*; bigeye tuna, *T. obesus*; little tunny, *Euthynnus alletteratus*; and frigate mackerel, *Auxis* sp. Sampling of landings took place between 26 September 1967 and 22 May 1968 at the ports of Dakar, Senegal; Freetown, Sierra Leone; Abidjan, Ivory Coast; Tema, Ghana; and Benguela, Angola. Samples were also taken from fish stored at a cannery in Mocamedes, Angola. Fish were captured by bait (pole-and-line) boats, purse seiners, and combinations of both. Only whole fish were used for this study, landed in fresh, iced, frozen, and indeterminate conditions. Fork lengths were usually measured to the nearest centimeter. Weight was usually measured to the nearest 0.1 kg. All nonmetric data were converted to centimeters and kilograms.

The allometric length-weight equation is used to describe the relation between length and weight:

$$W = aL^{b}e \qquad (1)$$

where W = weight in kilograms
L = length in centimeters
a and b = estimated parameters.
e = error term

Results

Estimates of a and b were made for each sample. A wide range in values of a and b occurred for the same species and, in some cases, for the identical sample category (category is defined as port, gear, and method of preservation of fish), that was at first alarming. However, examination of plots of the estimated curves revealed only minor differences among samples at sizes included in the samples. It was also noted that estimates of a are closely related to estimates of b (Figure 1), again indicating the fish at the same length weighed approximately the same.

Analyses of covariance were used to test the statistical significance of differences among length-weight relations within a sample category. F-tests for the significance of differences of the estimates of both parameters a and b[1] were made instead of F-tests for each parameter as is usually done, because I believe that the close relation between estimates of a and b demonstrates that no additional useful information would be obtained by making the separate tests. F-values for differences among samples within a category were almost always significant for all species with more than one sample. As mentioned previously, plots of the fitted lines showed only minor differences between samples for sizes found in both samples.

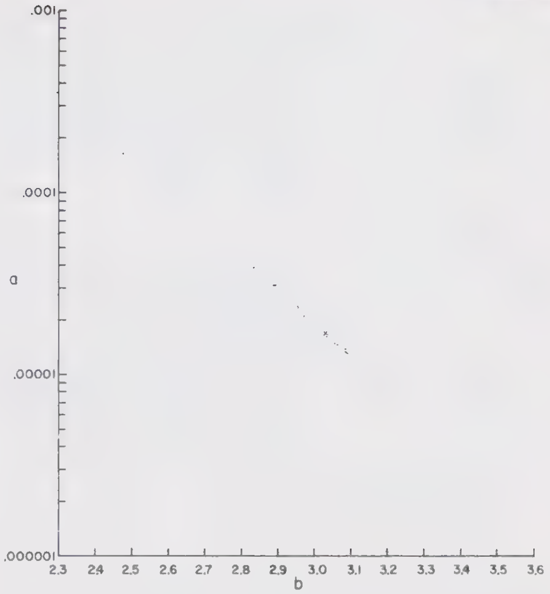

FIGURE 1.—Relation between estimates of a and b of the allometric length-weight relation from samples of Atlantic yellowfin tuna.

Analyses of covariance were also used to test whether differences among sample categories were present. Nested models were used because the significant differences among lines within sample categories indicated that samples rather than individual fish should be used to estimate the error term of the model. Only data for yellowfin and skipjack tunas were examined because there were insufficient data for the other species. Table 1 presents the analysis of covariance of differences among all sample categories for yellowfin tuna. The F-value for difference among sample categories is statistically significant at the

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[1] H_0; $a_i = a_j$ and $b_i = b_j$ where a_i = value of a from ith sample, b_i = value of b from ith sample and $i \neq j$.

TABLE 1.—Analysis of covariance of length-weight relation of yellowfin tuna.

Source	Degrees of freedom	Sum of squares	Mean square	*F*-value
Categories	24	1.321851	0.0550771	3.4115*
Samples within categories	128	2.066484	0.0161444	6.7748*
Residual	3,485	8.304751	0.0023830	
Total	3,637	11.693086		

*Significant at 1% level.

TABLE 2.—Analysis of covariance of length-weight relation of skipjack tuna.

Source	Degrees of freedom	Sum of squares	Mean square	*F*-value
Categories	20	2.560355	0.128018	5.0189*
Sample within categories	84	2.142605	0.0255072	7.3030*
Residuals	2,448	8.550099	0.0034927	
Total	2,552	13.253059		

*Significant at 1% level.

1% level. The *F*-value for difference among samples within a category is greater than that among categories. Table 2 presents results for skipjack tuna. Again the *F*-value is statistically significant at the 1% level, and the *F*-value among samples within categories is greater than that among categories. The reasons for the differences are not known. Although there was considerable overlap of sizes of fish encountered among the samples, size composition of the samples did differ and may have contributed to the differences in the length-weight relations because Equation (1) may not perfectly describe the length-weight relation for fish of all sizes. Figure 2 illustrates the variability found in the length-weight relations of yellowfin tuna. The variability among the relations increases with size as Equation (1) assumes.

Statistics of length-weight relations from combined samples for each species are presented in Table 3.

Discussion

Length-weight relations for yellowfin tuna from the Pacific (Chatwin, 1959), from the Atlantic (Poinsard, 1969), and from the present study are illustrated in Figure 3. There is reasonably close agreement among the three curves at small sizes. The Pacific yellowfin tuna appear to be heavier at larger sizes than fish from the Atlantic, but Chatwin did not include fish larger than 115 cm in his work. Two relations are used in Poinsard's work. A relation between fork length and predorsal length and one between predorsal length and weight. Poinsard tried several functions to explain the relations. In the case of fork length and predorsal length he chose the following function:

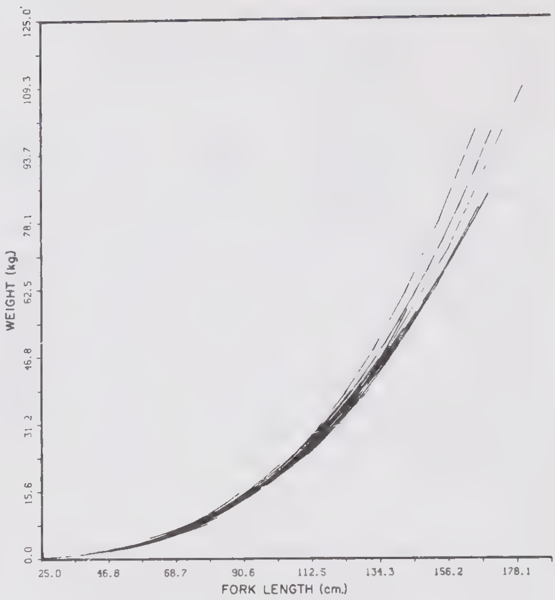

FIGURE 2.—Estimated length-weight relations for all sample categories of Atlantic yellowfin tuna.

$$LD_1 = -16.58774 + 4.66294\sqrt{L} \qquad (2)$$

where LD_1 = predorsal length

He based his choice on the fact that Equation (2) resulted in the highest value of r (correlation coefficient) of the several functions he tried. The value of r when Equation (2) was used was 0.99402, but when a power relation similar to Equation (1) was used the value of r (0.99386) is only slightly less. Figure 3 is based on the square root relation between fork length and predorsal length as recommended by Poinsard. It is very difficult, however, to interpret differences between r values when different dependent variables are used: predorsal length in one case, log (predorsal length) in the other. Equation (2) seems a poor choice because it implies that $LD_1 \leq 0$ when $L \leq 12.65$. The estimated weights using Poinsard's logarithmic relation are illustrated in Figure 4—the two curves are very similar for all lengths. This similarity indicates that the results of Poinsard and of this study are accurate estimates of the average length-weight relationship of eastern tropical Atlantic yellowfin tuna.

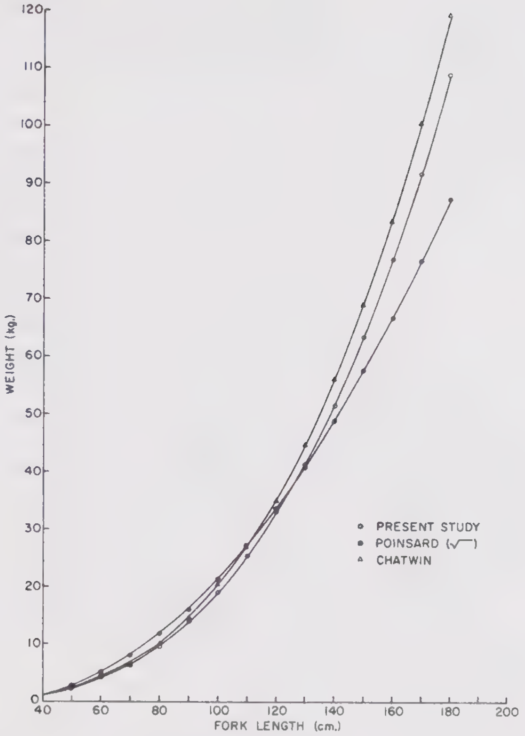

FIGURE 3.—Estimated length-weight relations for yellowfin tuna (Chatwin, 1959; Poinsard, 1969). Poinsard's relation based on square root relation between predorsal and fork length. Chatwin's study did not include fish longer than 115 cm.

Since it is desirable to utilize the function which was estimated directly from either predorsal or fork length data, the results of Poinsard should be used when predorsal lengths are measured and the results of the present study should be used when fork lengths are measured.

Beardsley[2] (pers. commun.) allowed me to examine length and weight measurements of more than 2,000 yellowfin tuna captured in the western Atlantic. These data are very similar to the data used in the present study.

Beardsley and Richards (1970) estimated the parameters of Equation (1) for skipjack tuna and little tunny captured off the coast of Florida. Their estimate of the equation for skipjack tuna is

$$W = 0.00007927L^{3.22750}$$

and for little tunny is

$$W = 0.0000181L^{3.02838}$$

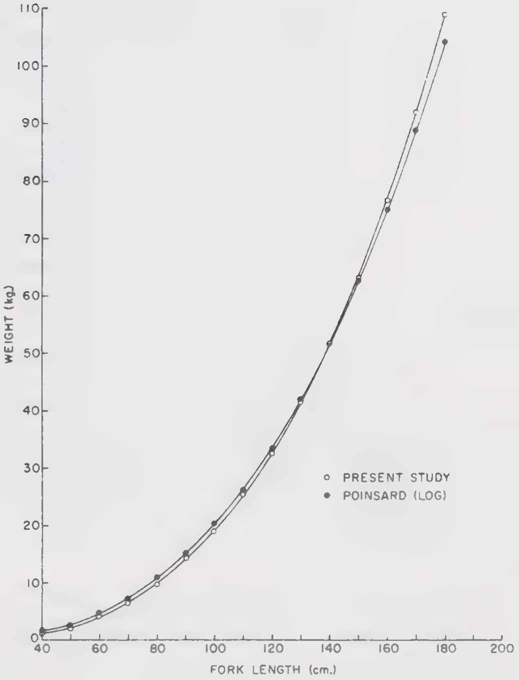

FIGURE 4.—Estimated length-weight relations for yellowfin tuna (Poinsard, 1969). Poinsard's relation based on logarithmic relation between predorsal and fork length.

These results are quite similar to the results of the present study. The range in fork length of skipjack tuna in their study was 38-78 cm and for little tunny 34-87 cm. Since these size ranges exceed the ranges encountered in this study their results should be used. Chatwin (1959) obtained similar results for skipjack tuna from the Pacific, and Batts (1972) for skipjack tuna from the western Atlantic.

The number of frigate mackerel used in this study is too small to produce very meaningful results. The results are presented here only to make them available to other workers.

Several authors including Pienaar and Thomson (1969) have questioned the validity of assumptions made about the error term in Equation (1). Also, the logarithmic transformation results in weight being slightly underestimated even if Equation (1) is correct. Results of simulations by Fox (1973)[3] indicate that b is unbiased and an unbiased estimate of a is given by

$$a' = a \exp\left(\tfrac{1}{2}\left(s^2{}_{W \cdot L}\right)\right) \qquad (3)$$

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[2] Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

[3] Fox, W. W., Jr. 1973. Some simple biologically useful functions and multiplicative error regression models. Unpubl. manuscr. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92037.

TABLE 3.—Statistics of length-weight relations for all data used in study.

Species	Number of fish	a	[1]b	Mean square error	Minimum fork length (cm)	Maximum fork length (cm)
Yellowfin tuna	3,689	0.000021804	2.96989	0.003265	40	170
Skipjack tuna	2,554	0.000005611	3.31497	0.005193	36	64
Bigeye tuna	190	0.000012494	3.12082	0.003405	41	132
Little tunny	753	0.000012000	3.08340	0.006935	41	57
Auxis sp.	50	0.000000280	4.13514	0.030871	30	45

[1] All estimates are significantly different than 0 at the 1% level.

where a' = unbiased estimate of a
$(s^2_{W \cdot L})$ = mean square error about the regression line.

The mean square errors for this study are low (Table 3). Thus the bias should be negligible. The results of this study were examined by comparing average weights of yellowfin used in the study against predicted weights. Differences were negligible as expected.

The significant differences found among samples and categories indicate that the variance of estimated numbers of fish caught, estimated from length frequency samples, could be reduced by a sophisticated sampling scheme which is stratified by category if not sample. Obviously it would be simpler to weigh fish from each sample rather than measure lengths, if one desired to stratify by sample. Logistics rule out this possibility. A formal cost-benefit analysis of the effort required to develop an adequate sampling scheme stratified by category probably would rule out this scheme. The significant differences among samples do point out the desirability of obtaining large numbers of samples rather than large sample sizes in further study of length-weight relations.

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AN EXAMINATION OF THE YIELD PER RECRUIT BASIS FOR A MINIMUM SIZE REGULATION FOR ATLANTIC YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

Some of the conceptual foundations of yield-per-recruit analysis as a management tool and as applied to the Atlantic yellowfin tuna fishery were critically explored. Problems examined include: (1) estimating the current state of the fishery in terms of a knife-edged recruitment approximation, (2) inferring consequences of management action from the yield-per-recruit isopleth, (3) the difficulty in achieving a maximum yield per recruit when there exist several gear types exploiting different size ranges, (4) the difficulty in obtaining projected increases in yield per recruit when the killing and discarding (dumping) of fish smaller than the optimum size occurs, and (5) the possible interaction between a size limit and the projection of the maximum sustainable yield.

In employing yield-per-recruit analysis to the Atlantic yellowfin tuna fishery, two approaches were taken—one approach makes use of a wide range of parameter estimates and a number of simplifying assumptions, but little data, and the other approach makes use of considerably more data, but is more confined in the parameter estimates and uses fewer of the simplifying assumptions. The general results of both approaches, assuming no dumping occurs, indicate that only minor increases in yield per recruit would occur if the size at recruitment is increased from our estimate of the present size at recruitment and fishing effort remains constant; an increase in fishing effort without changing other aspects of the fishery would not appreciably increase yield per recruit; and an increase in size at recruitment and in fishing effort would result in modest gains in yield per recruit. Specifically meeting the request of the International Commission for the Conservation of Atlantic Tunas, we recommended that a minimum size limit regulation in the vicinity of 55 cm (3.2 kg) be enacted.

The second regular meeting, in Madrid, Spain, on 2-7 December 1971, of the commission of ICCAT (International Commission for the Conservation of Atlantic Tunas) authorized the "Council to recommend to the Contracting Parties that they prohibit landing of yellowfin weighing less than a minimum weight somewhere between 3.2 and 10 kg." This recommendation was based on studies by members of the Subcommittee on Stock Assessment that showed that theoretically the size at first capture which maximizes the yield per recruit of yellowfin is between 10 and 25 kg.

A special ICCAT working group on stock assessment of yellowfin tuna met in Abidjan, Ivory Coast, 12-16 June 1972, to consider further scientific aspects of size regulation and other matters pertaining to the Atlantic yellowfin fishery (ICCAT, 1972).[2] Studies on yield per recruit were presented by Hayasi, Honma, and Suzuki (1972);[3] Joseph and Tomlinson (1972);[4] and Lenarz and Sakagawa (1972).[5] A similar study was published by Wise (1972)

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, LaJolla, CA 92037.

[2] ICCAT. 1972. Report of the meeting of the special working group on stock assessment of yellowfin tuna (Abidjan, June 12-16, 1972). Manuscript on file at ICCAT General Mola 17, Madrid, 1 Spain.

[3] Hayasi, S., M. Honma, and Z. Suzuki. 1972. A comment to rational utilization of yellowfin tuna and albacore stocks in the Atlantic Ocean. Far Seas Fisheries Research Laboratory, Orido 1000, Shimizu, Japan. Unpublished manuscript.

[4] Joseph, J., and P. K. Tomlinson. 1972. An evaluation of minimum size limits for Atlantic yellowfin. Inter-American Tropical Tuna Commission, La Jolla, Calif. Unpublished manuscript.

[5] Lenarz, W., and G. Sakagawa. 1972. A review of the yellowfin fishery of the Atlantic Ocean. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

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before the meeting. The report of the meeting may be considered as a summary of these papers, which indicated that increases in size at recruitment would probably increase yield per recruit but not by more than about 10%.

The special ICCAT working group also examined available evidence on the practicability of minimum size regulations. Scientists of the group were concerned that since the gears that fish for yellowfin in the Atlantic supposedly kill most fish that are captured, a minimum size regulation would reduce the number of small yellowfin that are landed but would not have the desired effect of reducing mortality rates of small yellowfin. This, of course, assumes that schools of yellowfin containing yellowfin less than any minimum size would actually be set upon. In this connection the group noted that the conditions which must be met before minimum size regulations can be effective are: (1) the fishermen must be able to estimate the size of yellowfin in a school, and (2) there must be little or no mixing of small yellowfin with large yellowfin within schools.

Very little evidence is available from the Atlantic on these subjects. Ten samples were presented at the Abidjan meeting that indicated considerable mixing of small yellowfin (<5 kg) with large yellowfin (>5 kg) within schools. The working group also took note of a study on the subject by Calkins (1965) when size regulations were being considered by the IATTC (Inter-American Tropical Tuna Commission) for the yellowfin fishery in the eastern tropical Pacific. Calkins, working with only one hypothetical minimum size out of a range of 12.7 to 25.0 kg, concluded that a 12.7-kg size regulation would be seriously complicated by size variation within sets. He also noted that a considerable amount of small yellowfin are often captured in sets that include skipjack. Thus it appears that it would not be possible to fish for skipjack without killing some small yellowfin. Evidence based on the few samples from the Atlantic indicated that sets would include yellowfin tuna larger and smaller than 5 kg; thus even if a minimum size regulation were set at this value it would be difficult to prevent the capture of fish smaller than 5 kg.

The working group recommended that more data should be collected on the subject from the Atlantic. The working group also noted that a reduction in the size at first recruitment should be prevented and that minimum size regulations of 3.2 kg that have been passed by several African nations should help prevent a reduction in size at recruitment.

The population dynamics of Atlantic yellowfin tuna are complex because the fishery is prosecuted by several types of gear: bait boats, small purse seiners, large purse seiners, and longliners. These gears tend to capture different sizes of fish and thus affect the population in different ways. FAO (1968) noted that longline gear tends to capture large yellowfin while the other gears capture small yellowfin. Lenarz (1970),[6] with more recent data, showed that American[7] purse seine gear tends to capture relatively more large yellowfin—in significant quantities—than was indicated for the earlier surface fishery. Joseph and Tomlinson (1972, see footnote 4) presented data that indicated small purse seiners of France-Ivory Coast-Senegal (FIS) tend to capture relatively more small yellowfin than the large FIS and American purse seiners. The differences among size selectivity of the four gears necessitates consideration of the physical makeup of the fleet when examining size regulations. Therefore, considerable attention was paid to this aspect of the problem during the study.

The above paragraph might be taken to imply that adequate data are available respecting the relative quantities and size distributions of fish caught by the various gears. It is our feeling that the adequacy of the data needs to be demonstrated. We cannot place much faith in the details of the relative size distributions per unit effort among the various fishing units, but we do feel that the general orders of magnitude are essentially correct. We should also point out that with the improvement in data over the last several years, the interpretations which accrue from the data and our appreciation of the considerable complexity of the fishery are more evident.

Definitions of Minimum Size

Because this paper discusses minimum size, it is necessary to define the term explicitly to avoid ambiguity and to prevent possible misapplications of the results of this study. "Minimum size" may be viewed from two aspects: absolute minimum size and effective minimum size. Absolute minimum size is defined as the smallest fish in the catch and is related to the concept of knife-edged recruitment in defining the size at recruitment to the fishery. Recruitment is defined as the act of becoming vulnerable to fishing. In the case of knife-edged recruitment, no fish are vulnerable to fishing prior to the size at recruitment. Fish that are larger than the size at recruitment are fully vulnerable to fishing. Since most recruitment is size specific, hence sequential, the term effective minimum size is also needed. Effective minimum size is that size whose corresponding age is used as the lower bound for integration of the yield equation as if recruitment were knife-edged, and which gives the same yield per recruit as the sequential recruitment case.

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[6] Lenarz, W. 1970. Estimates of yield per recruit of Atlantic yellowfin tuna. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[7] Refers to vessels registered in Canada, Panama, and the U.S.A.

Approaches to Yield-Per-Recruit Analysis

This paper examined several of the concepts involved in yield-per-recruit analyses because the question of what is the optimum minimum size for a given rate of exploitation is usually interpreted through such analyses. Both the classical approach, in which fishing mortality is constant with knife-edged recruitment, and the more complex approach, in which fishing mortality is size specific, are explored.

Throughout the paper we have intentionally kept mathematical notation to a bare minimum. We believe that most of the equations used are well known to readers actively involved in stock assessment. Readers who are not familiar with the equations can find excellent descriptions in the cited literature.

Employing the classical approach to yield-per-recruit analysis involves: (1) estimating the age or size at recruitment which represents an approximation of the current state of the fishery in terms of knife-edged recruitment; (2) finding the age or size at recruitment which maximizes the yield per recruit at a given level of fishing mortality; (3) imposing some regulation on the fishery such to achieve as its effective minimum size, the age or size at recruitment which maximizes the yield per recruit. The advice from the yield-per-recruit isopleth (in terms of the optimal age or size at recruitment) may be interpreted as either a knife-edged absolute minimum size or as an effective minimum size. Since for the fishery under consideration (and for many other fisheries as well) recruitment is not knife-edged, then we are talking about an effective minimum size. Now, on the other hand, if we assume that the absolute minimum size, the regulated size, and the effective minimum size are all the same, then we will have an inappropriate estimate of the yield per recruit, and the optimum may not be achieved. Somehow we need to determine the relationship between the effective minimum size and the regulated size; in some instances they can roughly be the same; but this equality will usually not obtain if the regulated size is chosen to be the absolute minimum size in the catch.

The more complex approach, which estimates size-specific fishing mortality, circumvents the first difficulty encountered in the classical approach, i.e., determining a knife-edged approximation to the current state of the fishery. The problem still remains, however, as to interpretation of the advice from the yield-per-recruit isopleth in terms of an effective minimum size. Joseph and Tomlinson (1972, see footnote 4) used the more complex approach in a recent study on minimum size regulations for the Atlantic yellowfin fishery. We have updated their analysis by using data made available at the Abidjan meeting and have also examined the sensitivity of the methodology to various sources of errors in the data.

DATA, PARAMETERS, AND COMPUTER PROGRAMS

Data

Catch- and length-frequency data for each type of gear for the 1967-71 period were obtained from the report of the meeting of the special ICCAT working group (Tables 10, 11, and 12 of ICCAT, 1972, see footnote 2) with the exception of length-frequency data of the 1967-68 FIS fishery and 1971 Japanese longline fishery. Length frequencies for the 1967-68 FIS fishery were compiled from various ORSTOM (Office de la Recherche Scientique et Technique Outre-Mer) publications (Lenarz and Sakagawa, 1972, see footnote 5). Length frequencies from the 1971 Japanese longline fishery are assumed to be the same as those of the 1970 Japanese longline fishery; this assumption appears justifiable because year to year changes in length frequencies from longline fisheries tend to be less than differences in length frequencies between longline fisheries and surface fisheries.

Length-frequency data were available only from the Japanese longline fishery, FIS surface fisheries, and American large purse seine fishery. Thus it was necessary to make several assumptions before estimating the length frequencies of the total catch of yellowfin in the Atlantic. Length frequencies for longline fisheries other than Japan are assumed to be the same as Japan's. Length frequencies for the bait boat and small purse seine fisheries other than FIS were assumed to be the same as the FIS fishery. Length frequencies for the large purse seine fisheries other than FIS and American were assumed to be the same as those two fisheries.

Parameters

The growth equation $[L = 194.8 \times (1 - e^{-0.42\,(t\,-\,0.62)})]$ presented in LeGuen and Sakagawa (1973) and length-weight relationship ($W = 0.0000214L^{2.9736}$) given by Lenarz (1971a)[8] were used, where L is fork length in cm, t is age in years, and W is weight in kg.

The annual instantaneous coefficient of natural mortality (M) is a difficult parameter to estimate and due to a lack of data only preliminary estimates have been made for the parameter in the Atlantic. We assume as most authors have that M is constant over the exploited phase. Estimates of $M = 2.61$ and 1.50 for the Atlantic were made by Pianet and LeHir (1971) based on data from bait boats and seiners, respectively. These estimates seem unreasonably high perhaps because their data were only from the Pointe Noire region which is a small area compared to the total region in the Atlantic where yellowfin tuna are found. Hennemuth (1961) estimated that M is 0.8 in the Pacific while Davidoff (1969) chose the upper bound of Hennemuth's estimate, 1.0. Hennemuth's work was based on estimates of instantaneous coefficient of total mortality (Z) made from age compositions of catches by primarily bait boats and an estimate of instantaneous coefficient of fishing mortality (F) from Schaefer (1957). Since bait boats appear to be selective for small yellowfin, F and Z are not constant, and methods of ageing yellowfin have not been proven correct, Hennemuth's estimate must be considered a first approximation. However, his estimate seems reasonably consistent with what is thought to be the life span of yellowfin. We assumed for the purposes of our calculations here that M is 0.8 as is conventional (based on Hennemuth's work in the Pacific); we also used values of 0.6 and 1.0 to encompass what we believe is the range of reasonable values.

Pianet and LeHir (1971) also estimated an average F of 0.88 for the segment of the Atlantic yellowfin tuna population that is exploited in the Pointe Noire region. As we have indicated, their estimate is not representative for the population as a whole.

Our range of estimates of Z for 1967-71 is 0.91 to 1.82 (Lenarz and Sakagawa, 1972, see footnote 5). If we assume that $M = 0.8$ for the Atlantic population, then F is 0.11 to 1.02. We believe that F is about 0.6 for recent years. However, we used a range of F values in our study.

Computer Programs

Most of the calculations were performed on the Burroughs 6700[9] computer at the University of California at San Diego. Programs used in the analysis, except for FRG708 (Paulik and Bayliff, 1967), were written by the authors; they are as follows:

1. Simplified Beverton and Holt yields per recuit—YPER.
2. Accuracy of knife-edged approximations of age at entry and interactions between minimum size and catch quota regulations—GXPOPS.
3. Yield-per-recruit isopleths under knife-edged recruitment—FRG708.

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[8] Lenarz, W. 1971a. Length-weight relations for five Atlantic scombrids. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

[9] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

4. Size-specific rates of fishing mortality—COHORT.
5. Yield-per-recruit isopleths for multigear fisheries with size-specific F—MGEAR.
6. Optimum size at recruitment under different levels of effort by two gears—OPSIZE.

ANALYSIS

As previously mentioned in the introduction, we use two approaches in analyzing the data, the knife-edged recruitment approach and the size-specific F approach.

Knife-Edged Recruitment Approach

Introduction

Two commonly used models for computing yield per recruit and determining the size at recruitment which maximizes yield per recruit are those of Beverton and Holt (1957) and Ricker (1958). We employed both models for knife-edged approximation analyses—the simplified Beverton and Holt model, making use of a wide range of parameter estimates or extrapolations from fisheries for similar species, and the Ricker model, making use of the best parameter estimates and giving a more detailed analysis of yield per recruit. We used the Ricker model instead of the Beverton and Holt model for calculating yield-per-recruit isopleths because the Ricker model allows the use of exponents in the length-weight relationship with values other than 3. It is important to stress that the material in the simplified Beverton and Holt model involves fewer assumptions than the material in subsequent sections. This is important because as our approach becomes more complex the data requirements become more rigorous. It can be argued that we have sufficient data for this simplified approach. In the more complex approaches this assertion becomes more tenuous; because we use more assumptions in the more complex approaches we do not necessarily obtain more information, even though it may appear that way. However, it should be noted that the assumption of a constant rate of mortality over the fishable life span contained in the simplified approach may be important, and we believe that it is not fulfilled. These analyses are followed by sections discussing the problems of determining the proper parameters which represent the current situation of the fishery.

Simplified Beverton and Holt Model

The Beverton and Holt yield-per-recruit model may be simplified such that relative yield per recruit, Y', is a function of three ratios:

$$C = l_r'/L_\infty$$
$$Q = M/K$$
$$E = F/(F + M)$$
$$Y' = Y/(RW_\infty)$$

and where l_r' is the size (length) at recruitment, W_∞, L_∞, and K are parameters of the von Bertalanffy growth equation, Y is yield in weight, and R is recruitment. Y' is tabulated in Beverton and Holt (1966), but more extensive calculations were performed with program YPER.[10] Beverton and Holt (1959) concluded that, within reason, there exists a common ratio between M and K within related species groups. Therefore, a range of estimates for the various parameters is utilized along with other information obtained by examining parameter estimates for M and K for yellowfin tuna from areas other than the Atlantic.

The range of values for the various parameters is as follows: $K = 0.28$ to 0.53 and $L_\infty = 175.2$ to 223.0 cm from LeGuen and Sakagawa (1973), $Z = 0.91$ to 1.82 from Lenarz and Sakagawa (1972, see footnote 5), and $M = 0.6$ to 1.0. From these ranges of estimates, a maximum range for E is 0.0 to 0.67 and for Q is 1.13 to 3.57. Using our most reasonable parameter estimates of $K = 0.42$, $M = 0.8$, and $Z = 1.4$, however, a reasonable range for E and Q was established by allowing either the numerator or denominator of the ratio to be one of our most reasonable estimates—the reasonable ranges are $E = 0.12$ to 0.56 and $Q = 1.42$ to 2.86. With $K = 0.42$, $M = 0.8$, and $Z = 1.4$, our most reasonable estimates of E and Q are 0.43 and 1.9, respectively.

Table 1 contains optimal values of size (cm) at recruitment, $l^{*\prime}_r$, for the maximum range of estimates of E and Q (deleting the impossible $E = 0.0$) for the range and most reasonable estimates of L_∞. The dashed lines enclose the

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[10] For some values of c, Table IIb of Beverton and Holt (1966) was slightly higher than computed by YPER; this may be due to differing methods of rounding.

Table 1.—Optimal values of size at recruitment (cm) as a function of the rate of exploitation (E) and the ratio of M to K (Q) for three estimates of L_∞.[1]

	E						
Q	0.1	0.2	0.3	0.4	0.5	0.6	0.7
				L_∞ = 175.2 cm			
1.0	56.6	73.1	84.4	94.3	102.3	109.5	115.8
1.5	49.4	64.1	74.8	83.4	90.8	97.1	102.8
2.0	43.8	57.1	66.9	74.8	81.5	87.2	92.5
2.5	39.4	51.7	60.4	67.8	73.9	79.4	84.1
3.0	35.9	47.1	55.4	62.0	67.6	72.7	77.1
3.5	32.9	43.3	51.0	57.1	62.4	66.9	71.1
				L_∞ = 194.8 cm			
1.0	62.9	81.2	94.3	104.8	113.8	121.8	128.8
1.5	54.9	71.3	83.2	92.7	100.9	107.9	114.4
2.0	48.7	63.5	74.4	83.2	90.6	97.0	102.8
2.5	43.8	57.5	67.2	75.4	82.2	88.2	93.5
3.0	39.9	52.4	61.6	69.0	75.2	80.8	85.7
3.5	36.6	48.1	56.7	63.5	69.4	74.4	79.1
				L_∞ = 223.0 cm			
1.0	72.0	93.0	107.9	120.0	130.2	139.4	147.4
1.5	62.9	81.6	95.2	106.2	115.5	123.5	130.9
2.0	55.8	72.7	85.2	95.2	103.7	111.0	117.7
2.5	50.2	65.8	76.9	86.3	94.1	101.0	107.0
3.0	45.7	60.0	70.5	78.9	86.1	92.6	98.1
3.5	41.9	55.1	64.9	72.7	79.4	85.2	90.5

[1] Dashed lines encompass our reasonable range of values; underlined value is our most reasonable estimate.

reasonable range of estimates (deleting the unreasonably low $E = 0.12$), and the underlined value in the center of Table 1 is our most reasonable estimate. One can see in Table 1 that the values are all greater than the approximate absolute minimum size of 32.5 cm[11] for the Atlantic yellowfin tuna fishery over the range of the estimates of L_∞.

For the moment let us assume that recruitment is knife-edged at 32.5 cm (0.67 kg) and that the fishery can be regulated such to obtain a knife-edged recruitment at any desired size. Therefore, the maximum possible increases in yield per recruit may be computed. Our smallest reasonable values for optimal size at recruitment are 47.1 cm (2.0 kg), 52.4 cm (2.8 kg), or 60.0 cm (4.1 kg) depending on L_∞. The respective predicted values of yield per recruit are 2.0%, 3.1%, and 4.3% higher than when size at recruitment is 32.5 cm. Our largest reasonable estimates of optimal size at recruitment are 97.1 cm (17 kg), 107.9 cm (24 kg), or 123.5 cm (36 kg). The respective predicted increases in yield per recruit are 65%, 73%, and 82%. The predicted increase in yield per recruit using all of our most reasonable parameter estimates, i.e., raising 32.5 cm to 83.2 cm (11 kg), is 23%. The bounds on an increase in yield per recruit, 2% to 82%, and the most likely value of 23%, are estimated under the assumptions of knife-edged recruitment, and that size at recruitment represents an absolute minimum size. The Atlantic yellowfin tuna fishery, however, does not have knife-edged recruitment.

We used equation 1b of this paper to obtain our most reasonable estimate of the 1967-71 average effective minimum size for the Atlantic yellowfin tuna fishery from average lengths given in Table 15 of Lenarz and Sakagawa (1972, see footnote 5). The estimate of average effective minimum size is about 55 cm (3.2 kg). Nearly all the values within the dashed lines in Table 1, however, are greater than 55. The only smallest reasonable estimate of optimal effective minimum size greater than 55 cm is 60.0 cm with L_∞ = 223.0 cm. An increase from 55 to 60.0 cm would give an increase in yield per recruit $< 0.2\%$. The largest reasonable estimates of optimal effective minimum size predict increases in yield per recruit of 28%, 36%, or 45% with increases from 55 cm to 97.1, 107.9, and 123.5 cm, respectively depending on L_∞. The increase in yield per recruit by increasing the effective minimum size from 55 to 83.2 cm, our most reasonable estimate, is only 7.9%.

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[11] The value of 32.5 cm represents our selection for an approximate absolute minimum size for the Atlantic yellowfin tuna fishery, which also agrees with that chosen by Joseph and Tomlinson (1972, see footnote 4).

From the above analysis using a wide range of parameter estimates, we can conclude with reasonable assurance that virtually any increase in the effective minimum size will cause an increase in yield per recruit. Our most likely estimate of this increase in yield per recruit is only 7.9% which is bounded, with reasonable parameter estimates, by 0% and 45%.

Ricker Model

Ricker model yield-per-recruit isopleths were calculated using values of M of 0.6, 0.8, and 1.0 to illustrate our estimates of actual (rather than relative) yield per recruit (Figures 1, 2, and 3). As will be mentioned in the next section it is difficult to estimate the location of the fishery on the graphs, i.e., when fishing mortality is size specific it is not a trivial matter to make reasonable estimates of age at recruitment, t_r', and a constant total mortality coefficient, Z. Our most reasonable estimates, taken from Lenarz and Sakagawa (1972, see footnote 5), of these parameters are: t_r' is 1.41 yr and Z is 1.4.

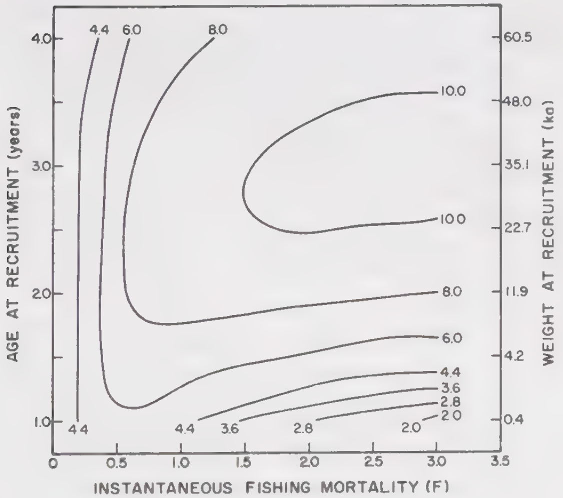

FIGURE 1.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.6$.

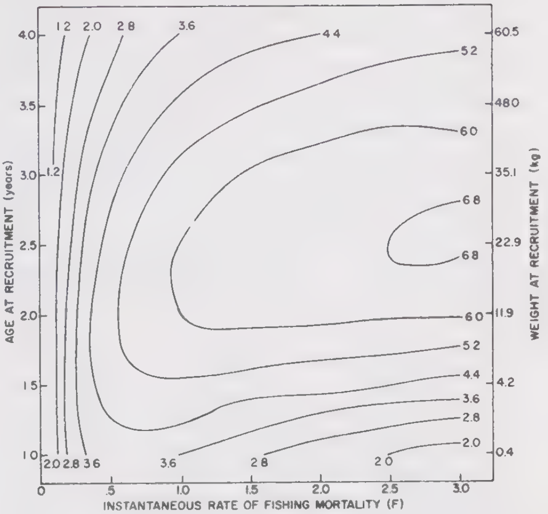

FIGURE 2.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 0.8$.

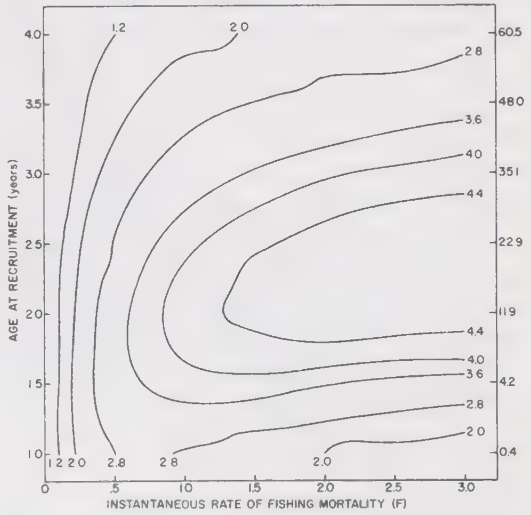

FIGURE 3.—Yield-per-recruit isopleths as functions of fishing mortality and age (and weight) at recruitment when $M = 1.0$.

The results (Figures 1, 2, and 3) show, for example, that with $M = 0.6$ and Z remaining constant (1.4), an increase in age at recruitment from 1.41 to 1.83 yr (or 77.5 cm) raises the yield per recruit about 20%; if $M = 0.8$, the same change raises the yield per recruit on the order of 10%; and if $M = 1.0$, the same change does not change yield per recruit. If age at recruitment is held constant and fishing mortality is doubled, when $M = 0.6$ yield per recruit decreases by some 20%; when $M = 0.8$ yield per recruit increases on the order of 5%; and when $M = 1.0$ yield per recruit increases about 30%. If effort is doubled and age at recruitment is raised to 1.83 yr, when $M = 0.6$ or $M = 0.8$ yield per recruit increases on the order of 20%; and when $M = 1.0$ yield per recruit increases by about 40%.

Estimation of t_r'

In employing a knife-edged approximation to size-specific recruitment protracted over some time period, the first problem is to determine the proper age at recruitment (t_r') such that the integration reflects the same yield per recruit as the size-specific recruitment case. There are two problems in doing so. First, there are two values for t_r' that will give the same yield per recruit as the size-specific recruitment case, unless eumetric fishing obtains. Often, however, this may be of little consequence, since one of the two values for t_r' could be obviously infeasible. Second, t_r' will depend on the fishing mortality.

Two estimators of t_r' are provided, at least implicitly, by Beverton and Holt (1957): (1) the age corresponding to the mean selection length, and (2) the resultant of a formula depending on Z and the average age, $\overline{t}$ (or average length, $\overline{l}$), in the catch. The mean selection length is the 50% selection length if the selection curve is symmetrical, and it is not dependent on the magnitude of the fishing mortality coefficient, F. The second estimator of t_r' is

$$t_r' = \overline{t} - 1/Z \qquad (1a)$$

or, in terms of length

$$l_r' = \overline{l} - K(L_\infty - \overline{l})/Z. \qquad (1b)$$

These two equations were obtained from manipulations of the Beverton and Holt yield equation.

Several computations of yield per recruit with the program GXPOPS were made utilizing $F = 0.1$ and $F = 2.0$, $M = 0.8$, the von Bertalanffy equation for Atlantic yellowfin tuna, and an arbitrary age-specific selection curve (Figure 4) in order to demonstrate the two problems and to evaluate the two estimators of t_r'. At $F = 0.1$, the values of t_r' giving the same yields per recruit as the selection curve are <8 mo (t_0 of the von Bertalanffy growth curve is 7.48 mo) or 24 mo, and 19 or 45 mo for $F = 2.0$. Since the state of the simulated fishery is not eumetric for either value of F, there are two knife-edged approximation locations. The effect of the magnitude of F on the true t_r' is obvious, with the lower value increasing from <8 to 19 mo and the upper value increasing from 24 to 45 mo as F is changed from 0.1 to 2.0. The reasonable values for t_r' to approximate the selection curve, however, are 24 mo for $F = 0.1$ and 19 mo for $F = 2.0$, a change of 5 mo.

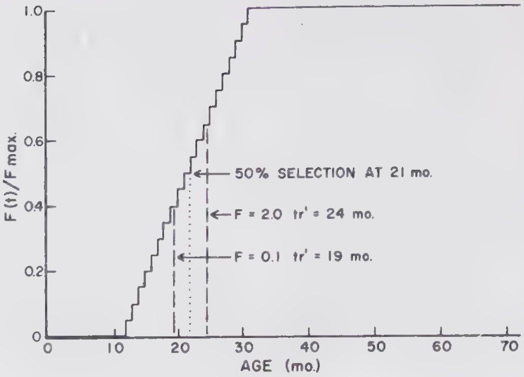

FIGURE 4.—Arbitrary age-specific recruitment curve.

Estimator 1, the mean selection age, is 21 mo and is shown along with the reasonable values in Figure 4. Using 21 mo for t_r' would result in yields per recruit that are 4% and 15% too high for $F = 0.1$ and $F = 2.0$ respectively. Estimator 1 does not change with F, of course, but in this case it lies intermediate between the true t_r' values. Estimator 2 gives 19 mo for $F = 0.1$ and 18 mo for $F = 2.0$. We emphasize that this estimator does depend on the magnitude of F.

Neither estimator is exact in this example where the catches, their ages, and the selection curve are known without error. This places doubt on their estimates from the usual catch at age data where considerable random error would be involved. Encouraging, though, is that both estimators indicate the proper direction that the fishery's selectivity should proceed to approach the optimal yield per recruit—about

15 mo for $F = 0.1$ and 30 mo for $F = 2.0$. Since estimator 1 requires size-selective data not frequently available and does not respond to changes in F, estimator 2 appears to be the most attractive for knife-edged approximations. The Atlantic yellowfin tuna fishery, however, has a much more complex recruitment pattern and size-specific F than this simple example owing to the diverse gear types. The mix of relative F among the various gear types makes the determination of the appropriate current t_r' somewhat tenuous.

Estimation of Constant Z

The yield-per-recruit isopleths shown in Figures 1, 2, and 3 were calculated under the assumption that fishing mortality and Z are constant after the fish are recruited. The value of Z was also estimated under the same assumption. The section on size-specific fishing mortality will indicate that F is not a constant, but is related to size. Thus our estimate of a constant Z may not be realistic but may be a more reasonable approach to estimating yield per recruit than the size-specific F approach given the quality of the data. It is the average of values of Z estimated for the FIS bait boat and purse seine fisheries (Lenarz and Sakagawa, 1972, see footnote 5). The size-specific F section indicates that F decreases with size for bait boats and increases with size for purse seiners. Beverton and Holt (1956) gave examples that indicated that when F decreases with age, constant Z will be overestimated and when F increases with age, constant Z will be underestimated. Hopefully we have obtained a reasonable estimate by taking the average of Z's for the two gears.

Size-Specific F Approach

Estimates of Length Frequencies

Length frequencies, numbers of yellowfin caught by 5-cm intervals starting at 35 cm (32.5 cm ≤ fork length <37.5 cm), were estimated for each gear and the total fishery for two overlapping periods, 1967-71 and 1969-71 (Figure 5). The first period was used with the hope that the effect caused by unequal strength of year classes would be minimized by averaging. The second period was used because it was felt that the data are more accurate. Length frequencies of the two periods are quite similar and produce similar estimates of size-specific fishing mortality and estimates of yield per recruit. Thus, to avoid redundancy, only the data for the 1967-71 period are used. Figure 6 and Table 2 show the length frequencies for each gear. The curves are as described earlier (see introductory section.)

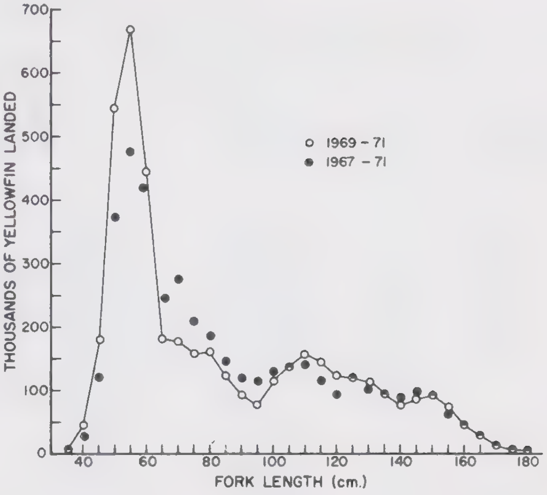

FIGURE 5.—Average length frequencies for the Atlantic yellowfin tuna fisheries for two periods, 1967-71 and 1969-71.

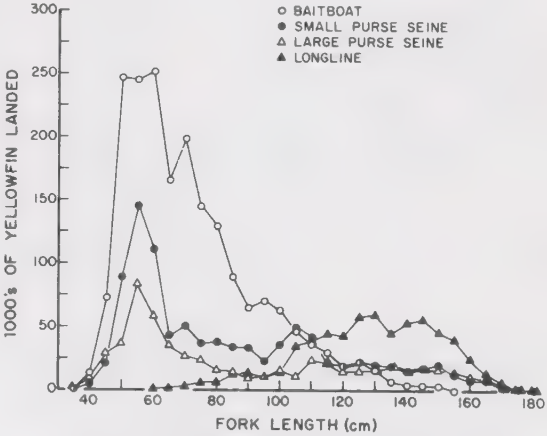

FIGURE 6.—Average length frequencies (1967-71) of Atlantic yellowfin tuna caught by four gear types.

Estimates of Size-Specific Fishing Mortality

Size-specific instantaneous coefficients of fishing mortality were estimated with the method of Gulland (1965) and Murphy (1965) as suggested

TABLE 2.—Basic data on size (age) composition of catch of yellowfin tuna from the tropical Atlantic Ocean.

Midpoint of size interval (cm)	Weight at beginning of interval (kg)	Age at beginning of interval (yr)	1967-71 average number of yellowfin landed				
			Bait boats	Small purse seiners	Large purse seiners	Longliners	Total
35	0.67	1.0579	1,886	372	100		2,358
40	1.03	1.1325	14,551	5,445	9,057		29,053
45	1.49	1.2093	72,972	21,782	28,372		123,126
50	2.08	1.2888	246,924	89,614	36,684	7	373,229
55	2.79	1.3710	245,206	146,883	83,153	22	475,264
60	3.66	1.4562	251,017	110,755	59,648	451	421,871
65	4.69	1.5445	165,328	42,427	35,891	647	244,293
70	5.90	1.6363	197,855	49,929	26,992	2,151	276,927
75	7.30	1.7317	143,885	36,942	23,263	5,435	209,525
80	8.90	1.8310	128,810	37,082	15,528	5,694	187,114
85	10.72	1.9348	89,637	31,143	13,338	12,025	146,143
90	12.77	2.0432	64,128	31,135	9,818	13,049	118,130
95	15.06	2.1568	70,422	22,248	10,062	11,665	114,397
100	17.61	2.2761	63,619	36,483	13,323	15,074	128,499
105	20.43	2.4017	45,582	48,274	11,647	34,071	139,574
110	23.54	2.5343	36,414	42,283	24,296	40,209	143,202
115	26.95	2.6748	29,227	21,268	21,466	44,034	115,995
120	30.67	2.8240	18,877	18,311	15,144	42,859	95,191
125	34.72	2.9832	22,228	23,711	15,018	57,358	118,915
130	39.10	3.1538	15,152	20,612	16,238	58,544	110,546
135	43.84	3.3376	7,142	18,304	18,504	44,690	88,640
140	48.95	3.5368	4,137	15,790	13,569	52,070	85,566
145	54.43	3.7542	3,393	17,301	17,886	55,582	94,162
150	60.31	3.9935	3,459	20,222	16,711	45,648	86,040
155	66.60	4.2595	1,511	12,057	14,926	39,108	67,602
160	73.30	4.5590	793	8,754	10,678	24,489	44,714
165	80.44	4.9017	634	7,803	6,633	13,659	28,729
170	88.03	5.3021	327	2,470	2,918	6,265	11,980
175	96.07	5.7838	209	2,132	1,383	241	3,965
180	104.59	6.3883	49	1,429	361	55	1,894
	113.60	7.2004					
Total			1,945,374	942,961	573,207	625,102	4,086,645

by Lenarz (1971b).[12] We followed the modification of Joseph and Tomlinson (1972, see footnote 4) by using the inverse of the von Bertalanffy growth equation to convert size distributions to age distributions. This method assumes that there is a reasonably accurate relationship between length and age of yellowfin tuna. This assumption has not been verified. Ageing by modal progression would probably be more satisfactory, if more complete length composition data were available on a monthly or quarterly basis.

The reverse iterative procedure with computer program COHORT and $M = 0.8$ was used to estimate size-specific values of fishing mortality (F) starting at the 180-cm interval. Four initial values of F were tried: 0.2, 0.4, 0.6, and 0.8 (Figure 7). Estimates of F tend to converge as size of the yellowfin tuna decreases with the range of initial values tried as is characteristic

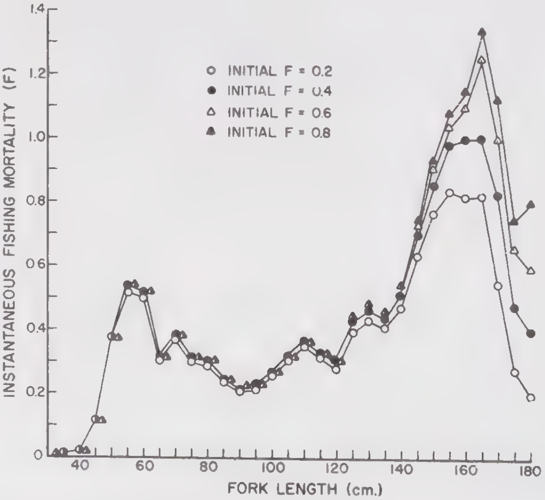

FIGURE 7.—Estimates of size-specific instantaneous fishing mortality coefficients (F) with several initial F values.

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[12] Lenarz, W. 1971b. Yield per recruit of Atlantic yellowfin tuna for multigear fisheries. Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif. Unpublished manuscript.

of the methodology (Tomlinson, 1970). Calculations of yield per recruit using initial values of F of 0.2 and 0.8 are shown in Figures 8 and 9 as functions of initial values of F, effort, and size at recruitment. The values of yield per recruit do not vary significantly ($< 10\%$) with changes in the initial values of F, and the relative values are quite similar. Values of size specific F are shown for each gear in Figure 10 when initial values of F are 0.2 and 0.8. When the initial value of F is 0.8, values of F for small purse seiners increase sharply with size from 170 to 180 cm. This does not occur when the initial value of F is 0.2. Intuitively we do not expect an increase in F with size past 170 cm and thus choose to use the results when the initial value of F is 0.2 in the remainder of the paper. Validity of the estimates of F depends on the validity of the assumption that recruitment has been fairly constant for the cohorts included in the analysis. The special ICCAT working group noted that the cohort which entered the surface fisheries in 1969 appears to be weaker than the following two cohorts (ICCAT, 1972, see footnote 2). Although inclusion of 5 yr of data in the analysis may minimize the source of error, future studies should examine the sensitivity of the results to errors of this type.

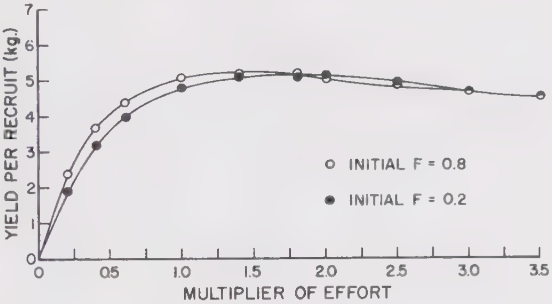

FIGURE 8.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, when size at recruitment is 32.5 cm, as a function of the multiplier of fishing effort.

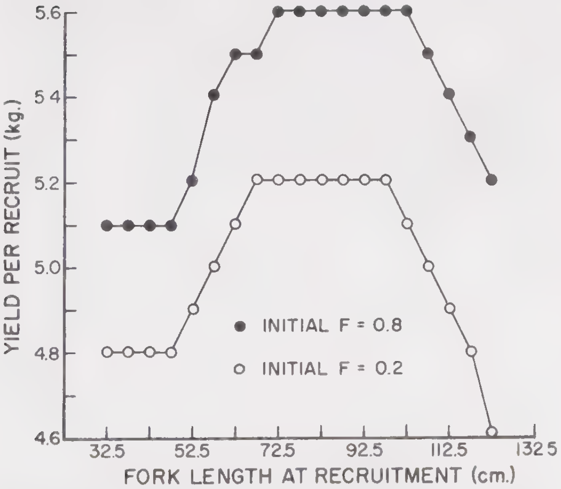

FIGURE 9.—Yield-per-recruit (kg) of Atlantic yellowfin tuna, with the current level of fishing effort, as a function of length at recruitment.

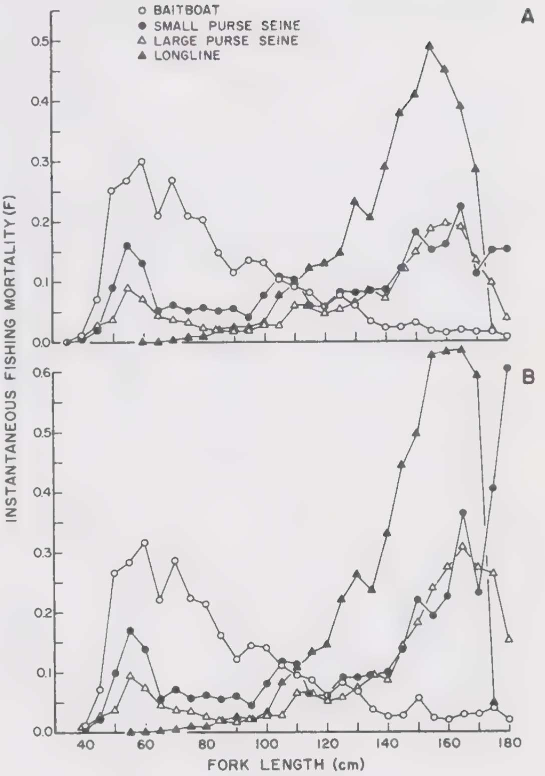

FIGURE 10.—Estimates of size-specific instantaneous fishing mortality coefficients (F) by gear type when initial values of F are (A) $F = 0.2$, (B) $F = 0.8$.

Estimates of Yield Per Recruit

Results of the yield-per-recruit calculations using the estimates of size-specific F when the initial value of F is 0.2 and with $M = 0.8$ are shown by gear in Table 3. Yield-per-recruit isopleths and the line of eumetric fishing (size at recruitment, $l^{*\prime}_{r}$, which maximizes yield per recruit at a given effort) for the entire fishery

TABLE 3.—Estimates of yield per recruit (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.08	0.15	0.21	0.31	0.39	0.46	0.49	0.56	0.62	0.68
117.5	30.6	0.09	0.17	0.24	0.36	0.46	0.54	0.58	0.66	0.73	0.80
112.5	26.9	0.11	0.21	0.29	0.43	0.55	0.65	0.69	0.80	0.89	0.96
107.5	23.5	0.13	0.24	0.33	0.50	0.64	0.75	0.80	0.92	1.02	1.11
102.5	20.4	0.15	0.27	0.38	0.57	0.73	0.86	0.92	1.06	1.17	1.27
97.5	17.6	0.17	0.31	0.44	0.66	0.85	1.01	1.08	1.24	1.38	1.50
92.5	15.0	0.19	0.35	0.50	0.75	0.96	1.15	1.23	1.41	1.58	1.72
87.5	12.7	0.20	0.38	0.54	0.81	1.04	1.24	1.32	1.52	1.69	1.84
82.5	10.7	0.22	0.41	0.58	0.88	1.12	1.34	1.43	1.64	1.82	1.98
77.5	8.9	0.24	0.45	0.63	0.95	1.22	1.45	1.55	1.78	1.97	2.13
72.5	7.3	0.26	0.48	0.68	1.02	1.30	1.54	1.64	1.87	2.07	2.23
67.5	5.9	0.27	0.51	0.72	1.08	1.38	1.62	1.73	1.96	2.14	2.30
62.5	4.7	0.29	0.53	0.75	1.12	1.41	1.65	1.76	1.98	2.16	2.30
57.5	3.7	0.30	0.56	0.78	1.15	1.43	1.66	1.76	1.96	2.11	2.22
52.5	2.8	0.31	0.57	0.79	1.15	1.42	1.63	1.72	1.88	2.00	2.08
47.5	2.1	0.31	0.58	0.80	1.15	1.42	1.61	1.69	1.84	1.94	2.00
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.60	1.68	1.82	1.91	1.97
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.96
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.34	0.58	0.75	0.97	1.09	1.16	1.19	1.24	1.28	1.31
117.5	30.6	0.35	0.60	0.77	0.99	1.11	1.18	1.21	1.27	1.30	1.33
112.5	26.9	0.36	0.61	0.79	1.01	1.13	1.20	1.23	1.28	1.31	1.34
107.5	23.5	0.38	0.64	0.83	1.06	1.20	1.28	1.32	1.38	1.43	1.47
102.5	20.4	0.40	0.67	0.87	1.12	1.27	1.37	1.41	1.49	1.55	1.60
97.5	17.6	0.41	0.69	0.89	1.14	1.30	1.40	1.44	1.52	1.59	1.64
92.5	15.0	0.41	0.70	0.90	1.15	1.30	1.39	1.43	1.50	1.56	1.61
87.5	12.7	0.42	0.71	0.91	1.16	1.31	1.40	1.44	1.51	1.56	1.60
82.5	10.7	0.42	0.71	0.91	1.16	1.30	1.39	1.43	1.49	1.53	1.57
77.5	8.9	0.43	0.71	0.91	1.15	1.29	1.37	1.40	1.45	1.49	1.51
72.5	7.3	0.43	0.71	0.91	1.14	1.27	1.34	1.36	1.41	1.43	1.44
67.5	5.9	0.43	0.72	0.91	1.13	1.24	1.30	1.32	1.35	1.36	1.35
62.5	4.7	0.43	0.71	0.90	1.11	1.22	1.27	1.28	1.30	1.29	1.28
57.5	3.7	0.43	0.71	0.90	1.10	1.19	1.23	1.24	1.24	1.23	1.21
52.5	2.8	0.44	0.72	0.89	1.08	1.16	1.19	1.20	1.19	1.17	1.14
47.5	2.1	0.44	0.71	0.89	1.06	1.13	1.15	1.15	1.14	1.11	1.07
42.5	1.5	0.44	0.71	0.88	1.06	1.12	1.14	1.14	1.11	1.08	1.05
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.54	0.69	0.89	0.99	1.05	1.07	1.10	1.12	1.12
117.5	30.6	0.32	0.55	0.71	0.90	1.01	1.06	1.08	1.11	1.12	1.13
112.5	26.9	0.33	0.56	0.73	0.92	1.03	1.09	1.11	1.14	1.16	1.17
107.5	23.5	0.34	0.58	0.74	0.94	1.04	1.10	1.12	1.15	1.17	1.18
102.5	20.4	0.34	0.58	0.74	0.93	1.02	1.06	1.08	1.10	1.10	1.10
97.5	17.6	0.35	0.58	0.74	0.92	1.00	1.04	1.05	1.06	1.06	1.06
92.5	15.0	0.35	0.58	0.73	0.91	0.99	1.02	1.03	1.03	1.03	1.02
87.5	12.7	0.35	0.58	0.73	0.90	0.97	1.00	1.00	1.00	0.99	0.97
82.5	10.7	0.35	0.58	0.73	0.89	0.96	0.98	0.98	0.97	0.95	0.93
77.5	8.9	0.35	0.58	0.72	0.88	0.93	0.95	0.95	0.93	0.91	0.88
72.5	7.3	0.35	0.57	0.72	0.86	0.92	0.92	0.92	0.90	0.87	0.84
67.5	5.9	0.35	0.57	0.71	0.85	0.89	0.89	0.88	0.86	0.82	0.79
62.5	4.7	0.35	0.57	0.71	0.84	0.87	0.87	0.86	0.83	0.80	0.76
57.5	3.7	0.35	0.57	0.70	0.82	0.85	0.84	0.82	0.79	0.75	0.71
52.5	2.8	0.35	0.57	0.69	0.80	0.82	0.80	0.79	0.75	0.71	0.67
47.5	2.1	0.35	0.56	0.68	0.78	0.79	0.77	0.75	0.71	0.66	0.62
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.75	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 3.—Estimates of yield per recruit (kg) when M = 0.8, initial F = 0.2, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

LONG LINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.40	1.86	2.49	2.87	3.12	3.21	3.38	3.49	3.57
117.5	30.6	0.82	1.44	1.90	2.53	2.90	3.14	3.23	3.38	3.47	3.54
112.5	26.9	0.84	1.46	1.93	2.54	2.90	3.12	3.19	3.32	3.39	3.43
107.5	23.5	0.85	1.48	1.93	2.52	2.84	3.02	3.08	3.17	3.20	3.21
102.5	20.4	0.86	1.48	1.93	2.49	2.78	2.93	2.97	3.03	3.03	3.01
97.5	17.6	0.86	1.47	1.90	2.43	2.69	2.81	2.83	2.85	2.82	2.76
92.5	15.0	0.86	1.46	1.89	2.38	2.62	2.71	2.72	2.71	2.66	2.58
87.5	12.7	0.86	1.46	1.87	2.34	2.55	2.62	2.63	2.59	2.52	2.43
82.5	10.7	0.86	1.45	1.85	2.29	2.48	2.52	2.52	2.46	2.36	2.25
77.5	8.9	0.85	1.43	1.82	2.23	2.38	2.40	2.38	2.29	2.17	2.04
72.5	7.3	0.85	1.41	1.79	2.17	2.29	2.28	2.24	2.13	1.99	1.85
67.5	5.9	0.84	1.39	1.75	2.09	2.18	2.13	2.09	1.95	1.79	1.63
62.5	4.7	0.84	1.38	1.72	2.03	2.09	2.03	1.98	1.82	1.64	1.48
57.5	3.7	0.83	1.35	1.67	1.95	1.97	1.88	1.81	1.63	1.44	1.27
52.5	2.8	0.82	1.33	1.63	1.86	1.85	1.73	1.66	1.46	1.26	1.09
47.5	2.1	0.82	1.31	1.60	1.81	1.77	1.64	1.56	1.35	1.15	0.98
42.5	1.5	0.82	1.31	1.59	1.79	1.75	1.61	1.53	1.32	1.12	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

are shown in Figure 11. Table 3 and Figures 8, 9, and 11 indicate that if size at recruitment remains constant at 32.5 cm, very little increase in yield per recruit (~5%) can be expected if effort is increased, and if effort remains constant, very little (~10%) increase in yield per recruit can be expected by increasing size at recruitment. However, if fishing effort is doubled (i.e., multiplier = 2.0) and size at recruitment increased to 55 cm (3.2 kg), yield per recruit would increase 15%, or if size at recruitment is increased to 77.5 cm (~10 kg), yield per recruit would increase about 30% (Table 3). Since the line of eumetric fishing shows that optimum size at recruitment changes with fishing effort, any "minimum size" regulation must be geared to fishing effort.

If fishermen are unable to distinguish the size of yellowfin before capturing them and a minimum size regulation prevents their landing, then the discarding of dead yellowfin will occur. Table 4 presents landings per recruit by gear and Figure 12 the landings per recruit for the total fishery when killing and discarding ("dumping") of all yellowfin smaller than the size limit occurs. If the minimum size limit is 55 cm and effort remains the same, then a 2.7% decrease in landings per recruit would occur; and a 13% decrease in landings per recruit would occur if the minimum size is set at 77.5 cm. If effort is doubled and the minimum size is 55 cm, then a 1% increase in landings per recruit would occur; with a minimum size of 77.5 cm, a 16% decline in landings per recruit would

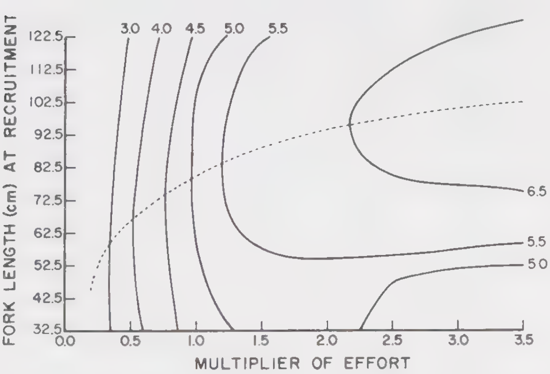

FIGURE 11.—Yield-per-recruit (kg) isopleths for the entire Atlantic yellowfin tuna fishery. Dotted curve is the line of eumetric fishing.

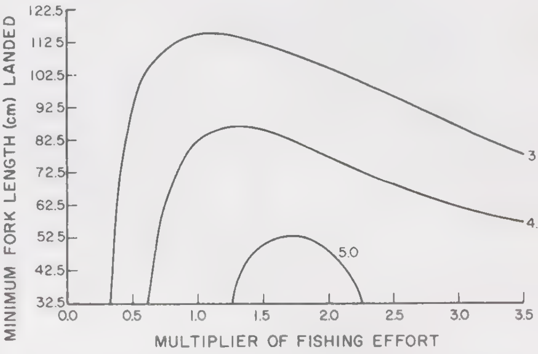

FIGURE 12.—Landings-per-recruit (kg) isopleths for Atlantic yellowfin tuna when all fish less than the minimum size that are caught are discarded dead.

TABLE 4.—Landings per recruit (kg) when $M = 0.8$, initial $F_t = 0.2$, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.07	0.12	0.15	0.18	0.18	0.17	0.16	0.14	0.12	0.10
117.5	30.6	0.08	0.14	0.18	0.22	0.22	0.22	0.21	0.19	0.16	0.14
112.5	26.9	0.10	0.17	0.22	0.27	0.29	0.28	0.28	0.25	0.22	0.19
107.5	23.5	0.12	0.20	0.26	0.33	0.36	0.36	0.36	0.33	0.30	0.27
102.5	20.4	0.14	0.24	0.31	0.40	0.44	0.45	0.44	0.42	0.39	0.35
97.5	17.6	0.16	0.27	0.36	0.48	0.53	0.56	0.56	0.54	0.51	0.47
92.5	15.0	0.18	0.31	0.41	0.55	0.63	0.66	0.67	0.66	0.63	0.59
87.5	12.7	0.19	0.34	0.45	0.61	0.70	0.74	0.75	0.75	0.73	0.69
82.5	10.7	0.21	0.37	0.50	0.68	0.79	0.84	0.86	0.87	0.85	0.81
77.5	8.9	0.23	0.41	0.55	0.76	0.89	0.97	0.99	1.01	1.00	0.97
72.5	7.3	0.25	0.44	0.60	0.84	0.99	1.08	1.11	1.15	1.15	1.12
67.5	5.9	0.27	0.48	0.66	0.92	1.10	1.22	1.25	1.31	1.33	1.32
62.5	4.7	0.28	0.51	0.70	0.98	1.18	1.31	1.35	1.43	1.46	1.46
57.5	3.7	0.29	0.54	0.74	1.05	1.27	1.42	1.48	1.57	1.62	1.64
52.5	2.8	0.30	0.56	0.77	1.10	1.34	1.51	1.57	1.69	1.76	1.79
47.5	2.1	0.31	0.57	0.79	1.14	1.39	1.58	1.65	1.79	1.87	1.92
42.5	1.5	0.31	0.58	0.80	1.15	1.41	1.59	1.67	1.81	1.90	1.95
37.5	1.0	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95
32.5	0.7	0.31	0.58	0.80	1.15	1.41	1.60	1.67	1.81	1.90	1.95

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.31	0.47	0.54	0.56	0.50	0.43	0.40	0.31	0.25	0.19
117.5	30.6	0.32	0.49	0.57	0.60	0.55	0.48	0.44	0.36	0.29	0.23
112.5	26.9	0.33	0.51	0.60	0.64	0.59	0.53	0.49	0.41	0.33	0.27
107.5	23.5	0.35	0.55	0.65	0.71	0.68	0.62	0.58	0.50	0.42	0.35
102.5	20.4	0.37	0.58	0.70	0.78	0.76	0.71	0.68	0.60	0.52	0.45
97.5	17.6	0.38	0.61	0.73	0.82	0.81	0.77	0.74	0.66	0.59	0.51
92.5	15.0	0.39	0.62	0.75	0.84	0.84	0.80	0.78	0.70	0.62	0.55
87.5	12.7	0.40	0.63	0.76	0.87	0.88	0.84	0.82	0.75	0.67	0.60
82.5	10.7	0.40	0.64	0.78	0.90	0.91	0.88	0.85	0.79	0.71	0.64
77.5	8.9	0.41	0.65	0.80	0.92	0.94	0.91	0.89	0.83	0.76	0.69
72.5	7.3	0.41	0.66	0.81	0.94	0.96	0.94	0.92	0.86	0.79	0.73
67.5	5.9	0.42	0.67	0.82	0.96	0.99	0.98	0.96	0.90	0.84	0.77
62.5	4.7	0.42	0.68	0.83	0.98	1.01	1.00	0.98	0.93	0.87	0.81
57.5	3.7	0.43	0.69	0.85	1.01	1.05	1.05	1.04	1.00	0.95	0.89
52.5	2.8	0.43	0.70	0.87	1.04	1.10	1.10	1.10	1.07	1.03	0.98
47.5	2.1	0.44	0.71	0.88	1.05	1.11	1.13	1.13	1.10	1.07	1.03
42.5	1.5	0.44	0.71	0.88	1.05	1.12	1.13	1.13	1.11	1.08	1.04
37.5	1.0	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04
32.5	0.7	0.44	0.71	0.88	1.06	1.12	1.13	1.13	1.11	1.08	1.04

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.28	0.43	0.50	0.51	0.46	0.39	0.36	0.28	0.21	0.16
117.5	30.6	0.29	0.45	0.52	0.54	0.50	0.43	0.39	0.31	0.25	0.19
112.5	26.9	0.30	0.47	0.55	0.59	0.54	0.48	0.44	0.36	0.29	0.24
107.5	23.5	0.31	0.49	0.58	0.63	0.59	0.53	0.50	0.42	0.35	0.28
102.5	20.4	0.32	0.50	0.59	0.64	0.61	0.55	0.52	0.44	0.37	0.31
97.5	17.6	0.32	0.51	0.60	0.66	0.63	0.57	0.54	0.46	0.39	0.33
92.5	15.0	0.33	0.51	0.61	0.67	0.64	0.59	0.56	0.48	0.41	0.35
87.5	12.7	0.33	0.52	0.62	0.68	0.65	0.60	0.57	0.50	0.42	0.36
82.5	10.7	0.33	0.52	0.62	0.69	0.67	0.62	0.59	0.51	0.44	0.38
77.5	8.9	0.33	0.53	0.63	0.70	0.68	0.63	0.60	0.53	0.46	0.40
72.5	7.3	0.34	0.53	0.64	0.71	0.70	0.65	0.62	0.55	0.49	0.43
67.5	5.9	0.34	0.54	0.65	0.72	0.71	0.67	0.64	0.57	0.51	0.45
62.5	4.7	0.34	0.54	0.65	0.74	0.73	0.69	0.66	0.60	0.54	0.48
57.5	3.7	0.35	0.55	0.66	0.75	0.75	0.71	0.69	0.63	0.58	0.53
52.5	2.8	0.35	0.56	0.68	0.77	0.77	0.74	0.73	0.67	0.62	0.58
47.5	2.1	0.35	0.56	0.68	0.77	0.78	0.75	0.74	0.69	0.64	0.60
42.5	1.5	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
37.5	1.0	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61
32.5	0.7	0.35	0.56	0.68	0.78	0.79	0.76	0.74	0.70	0.65	0.61

TABLE 4.—Landings per recruit (kg) when M = 0.8, initial F = 0.2, growth curve of LeGuen and Sakagawa (1973) is used, and yellowfin less than the minimum size are caught and discarded dead.—Continued.

MINIMUM SIZE		LONG LINERS MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.72	1.13	1.34	1.43	1.33	1.16	1.07	0.85	0.67	0.52
117.5	30.6	0.74	1.18	1.41	1.53	1.43	1.27	1.18	0.96	0.76	0.60
112.5	26.9	0.77	1.22	1.47	1.61	1.53	1.37	1.28	1.06	0.86	0.69
107.5	23.5	0.79	1.25	1.51	1.68	1.61	1.45	1.37	1.15	0.94	0.77
102.5	20.4	0.80	1.28	1.55	1.72	1.67	1.52	1.43	1.21	1.01	0.84
97.5	17.6	0.81	1.29	1.56	1.74	1.69	1.54	1.46	1.24	1.04	0.86
92.5	15.0	0.81	1.29	1.57	1.76	1.70	1.56	1.48	1.26	1.06	0.88
87.5	12.7	0.81	1.30	1.58	1.77	1.72	1.58	1.49	1.28	1.08	0.90
82.5	10.7	0.81	1.30	1.58	1.78	1.73	1.59	1.51	1.30	1.10	0.92
77.5	8.9	0.82	1.31	1.59	1.78	1.74	1.60	1.51	1.30	1.10	0.93
72.5	7.3	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.93
67.5	5.9	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
62.5	4.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
57.5	3.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
52.5	2.8	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
47.5	2.1	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
42.5	1.5	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
37.5	1.0	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94
32.5	0.7	0.82	1.31	1.59	1.78	1.74	1.60	1.52	1.31	1.11	0.94

occur. Therefore, if effort is constant the predicted gain with no dumping is greater than the possible loss through dumping if the minimum size were 55 cm, but at 77.5 cm the opposite is true. At both size limits we predict a greater gain with no dumping than possible loss through dumping if effort is doubled.

Assuming constant recruitment, yield per recruit per unit effort is a measure of fishing success. Table 5 presents the estimated yield per recruit per effort by gear assuming no dumping. Increasing the size at recruitment to 77.5 cm at the current level of effort would result in a 17% decrease for bait boats, a 9% increase for small purse seiners, a 12% increase for large purse seiners, and a 25% increase for longliners. Yield per recruit per effort would drop by about 35% for each of the gears if effort doubled and size at recruitment increased to 77.5 cm. If effort doubled and size at recruitment remained 32.5 cm, yield per recruit per effort would decrease by 30% for bait boats, 50% for purse seiners, and 60% for longliners.

Changes in the average weight of landings should be considered because average weight affects the values of landings particularly in light of size-specific changes in the value of yellowfin tuna. Table 6 presents estimates of the average weight of catches by gear. Figure 13 shows average weight isopleths for the entire fishery. If effort remained constant and size at recruitment increased to 77.5 cm, the average weight of the catch of the total fishery would increase from 17.7 kg to 30.3 kg. If effort doubled and size at recruitment increased to 77.5 cm, the average weight would increase to 24.2 kg.

Sensitivity of Results to Errors when Ageing Large Yellowfin

The growth curve used in this study was based on the use of modal progressions to age yellowfin. Unfortunately while this method is probably reasonably accurate for ageing yellowfin less than about 130 cm long, beyond this size it becomes increasingly difficult to separate modes, and there is a reasonable probability that ages are increasingly underestimated with increases in size. In addition, because tuna apparently spawn over a large portion of the year, the exact meaning of age is not always clear. Alternative methods, such as ageing by

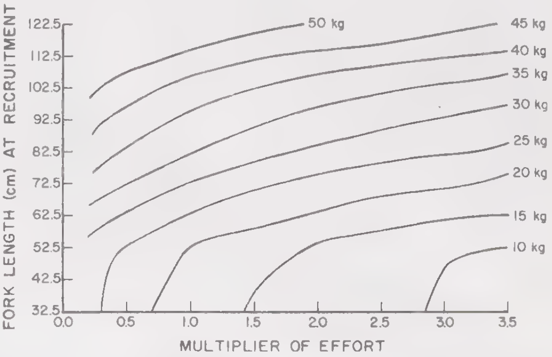

FIGURE 13.—Average weight (kg) isopleths for the entire Atlantic yellowfin tuna fishery.

TABLE 5.—Estimates of yield per recruit per effort (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.40	0.37	0.35	0.31	0.28	0.25	0.24	0.22	0.21	0.19
117.5	30.6	0.47	0.43	0.40	0.36	0.33	0.30	0.29	0.26	0.24	0.23
112.5	26.9	0.55	0.51	0.48	0.43	0.39	0.36	0.35	0.32	0.30	0.28
107.5	23.5	0.64	0.60	0.56	0.50	0.45	0.42	0.40	0.37	0.34	0.32
102.5	20.4	0.73	0.68	0.64	0.57	0.52	0.48	0.46	0.42	0.39	0.36
97.5	17.6	0.84	0.78	0.74	0.66	0.61	0.56	0.54	0.50	0.46	0.43
92.5	15.0	0.94	0.88	0.83	0.75	0.69	0.64	0.61	0.57	0.53	0.49
87.5	12.7	1.01	0.95	0.90	0.81	0.74	0.69	0.66	0.61	0.56	0.53
82.5	10.7	1.09	1.03	0.97	0.88	0.80	0.74	0.72	0.66	0.61	0.57
77.5	8.9	1.19	1.12	1.06	0.95	0.87	0.81	0.78	0.71	0.66	0.61
72.5	7.3	1.28	1.20	1.13	1.02	0.93	0.85	0.82	0.75	0.69	0.64
67.5	5.9	1.37	1.28	1.21	1.08	0.98	0.90	0.86	0.78	0.71	0.66
62.5	4.7	1.43	1.34	1.25	1.12	1.01	0.92	0.88	0.79	0.72	0.66
57.5	3.7	1.49	1.39	1.30	1.15	1.02	0.92	0.88	0.78	0.70	0.64
52.5	2.8	1.54	1.42	1.32	1.15	1.02	0.91	0.86	0.75	0.67	0.60
47.5	2.1	1.57	1.44	1.33	1.15	1.01	0.90	0.84	0.74	0.65	0.57
42.5	1.5	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.73	0.64	0.56
37.5	1.0	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56
32.5	0.7	1.57	1.44	1.33	1.15	1.01	0.89	0.84	0.72	0.63	0.56

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.72	1.46	1.26	0.97	0.78	0.65	0.60	0.50	0.43	0.38
117.5	30.6	1.77	1.50	1.29	0.99	0.79	0.66	0.61	0.51	0.43	0.38
112.5	26.9	1.82	1.54	1.31	1.01	0.80	0.67	0.61	0.51	0.44	0.38
107.5	23.5	1.91	1.61	1.38	1.06	0.85	0.71	0.66	0.55	0.48	0.42
102.5	20.4	1.99	1.69	1.45	1.12	0.90	0.76	0.70	0.59	0.52	0.46
97.5	17.6	2.05	1.73	1.48	1.14	0.93	0.78	0.72	0.61	0.53	0.47
92.5	15.0	2.07	1.74	1.49	1.15	0.93	0.77	0.72	0.60	0.52	0.46
87.5	12.7	2.10	1.76	1.51	1.16	0.93	0.78	0.72	0.60	0.52	0.46
82.5	10.7	2.12	1.78	1.52	1.16	0.93	0.77	0.71	0.60	0.51	0.45
77.5	8.9	2.13	1.78	1.52	1.15	0.92	0.76	0.70	0.58	0.50	0.43
72.5	7.3	2.14	1.79	1.52	1.14	0.91	0.74	0.68	0.56	0.48	0.41
67.5	5.9	2.15	1.79	1.51	1.13	0.89	0.72	0.66	0.54	0.45	0.39
62.5	4.7	2.16	1.78	1.50	1.11	0.87	0.70	0.64	0.52	0.43	0.37
57.5	3.7	2.17	1.79	1.50	1.10	0.85	0.68	0.62	0.50	0.41	0.35
52.5	2.8	2.19	1.79	1.49	1.08	0.83	0.66	0.60	0.48	0.39	0.33
47.5	2.1	2.19	1.78	1.48	1.06	0.81	0.64	0.58	0.45	0.37	0.31
42.5	1.5	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.45	0.36	0.30
37.5	1.0	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30
32.5	0.7	2.19	1.78	1.47	1.06	0.80	0.63	0.57	0.44	0.36	0.30

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	1.57	1.34	1.16	0.89	0.71	0.58	0.53	0.44	0.37	0.32
117.5	30.6	1.61	1.37	1.18	0.90	0.72	0.59	0.54	0.44	0.37	0.32
112.5	26.9	1.66	1.41	1.21	0.92	0.74	0.60	0.55	0.46	0.39	0.33
107.5	23.5	1.71	1.44	1.24	0.94	0.75	0.61	0.56	0.46	0.39	0.34
102.5	20.4	1.72	1.44	1.23	0.93	0.73	0.59	0.54	0.44	0.37	0.32
97.5	17.6	1.73	1.45	1.23	0.92	0.72	0.58	0.53	0.43	0.35	0.30
92.5	15.0	1.74	1.45	1.22	0.91	0.71	0.57	0.51	0.41	0.34	0.29
87.5	12.7	1.74	1.45	1.22	0.90	0.69	0.56	0.50	0.40	0.33	0.28
82.5	10.7	1.74	1.44	1.21	0.89	0.68	0.54	0.49	0.39	0.32	0.27
77.5	8.9	1.75	1.44	1.20	0.88	0.67	0.53	0.47	0.37	0.30	0.25
72.5	7.3	1.75	1.44	1.20	0.86	0.65	0.51	0.46	0.36	0.29	0.24
67.5	5.9	1.75	1.43	1.19	0.85	0.64	0.49	0.44	0.34	0.27	0.23
62.5	4.7	1.76	1.43	1.18	0.84	0.62	0.48	0.43	0.33	0.27	0.22
57.5	3.7	1.76	1.42	1.17	0.82	0.60	0.46	0.41	0.32	0.25	0.20
52.5	2.8	1.76	1.42	1.15	0.80	0.59	0.45	0.40	0.30	0.24	0.19
47.5	2.1	1.76	1.40	1.14	0.78	0.57	0.43	0.38	0.29	0.22	0.18
42.5	1.5	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.18
37.5	1.0	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17
32.5	0.7	1.76	1.40	1.14	0.78	0.56	0.42	0.37	0.28	0.22	0.17

TABLE 5.—Estimates of yield per recruit per effort (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

LONG LINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	4.00	3.51	3.10	2.49	2.05	1.74	1.61	1.35	1.16	1.02
117.5	30.6	4.12	3.60	3.17	2.53	2.07	1.75	1.61	1.35	1.16	1.01
112.5	26.9	4.21	3.66	3.21	2.54	2.07	1.73	1.60	1.33	1.13	0.98
107.5	23.5	4.27	3.69	3.22	2.52	2.03	1.68	1.54	1.27	1.07	0.92
102.5	20.4	4.31	3.70	3.21	2.49	1.99	1.63	1.49	1.21	1.01	0.86
97.5	17.6	4.31	3.68	3.17	2.43	1.92	1.56	1.42	1.14	0.94	0.79
92.5	15.0	4.30	3.66	3.14	2.38	1.87	1.50	1.36	1.08	0.89	0.74
87.5	12.7	4.30	3.64	3.11	2.34	1.82	1.46	1.31	1.04	0.84	0.69
82.5	10.7	4.29	3.61	3.08	2.29	1.77	1.40	1.26	0.98	0.79	0.64
77.5	8.9	4.27	3.57	3.03	2.23	1.70	1.33	1.19	0.92	0.72	0.58
72.5	7.3	4.24	3.53	2.98	2.17	1.63	1.26	1.12	0.85	0.66	0.53
67.5	5.9	4.21	3.49	2.91	2.09	1.55	1.19	1.05	0.78	0.60	0.47
62.5	4.7	4.19	3.45	2.86	2.03	1.49	1.13	0.99	0.73	0.55	0.42
57.5	3.7	4.15	3.39	2.79	1.95	1.40	1.04	0.91	0.65	0.49	0.36
52.5	2.8	4.12	3.33	2.72	1.86	1.32	0.96	0.83	0.58	0.42	0.31
47.5	2.1	4.09	3.29	2.67	1.81	1.26	0.91	0.78	0.54	0.38	0.28
42.5	1.5	4.08	3.27	2.65	1.79	1.25	0.89	0.76	0.53	0.37	0.27
37.5	1.0	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27
32.5	0.7	4.08	3.27	2.65	1.78	1.24	0.89	0.76	0.52	0.37	0.27

ENTIRE FISHERY

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	7.70	6.68	5.86	4.65	3.82	3.22	2.98	2.51	2.17	1.91
117.5	30.6	7.97	6.90	6.04	4.78	3.91	3.29	3.05	2.57	2.21	1.94
112.5	26.9	8.25	7.12	6.22	4.90	4.00	3.36	3.11	2.61	2.25	1.97
107.5	23.5	8.53	7.34	6.40	5.02	4.08	3.42	3.16	2.65	2.27	1.99
102.5	20.4	8.75	7.51	6.53	5.10	4.14	3.46	3.19	2.67	2.28	2.00
97.5	17.6	8.92	7.64	6.62	5.16	4.17	3.48	3.20	2.67	2.28	1.99
92.5	15.0	9.04	7.73	6.69	5.19	4.19	3.48	3.21	2.67	2.27	1.98
87.5	12.7	9.14	7.80	6.74	5.21	4.19	3.48	3.20	2.65	2.26	1.96
82.5	10.7	9.24	7.86	6.78	5.22	4.18	3.46	3.18	2.62	2.22	1.92
77.5	8.9	9.34	7.92	6.81	5.22	4.16	3.42	3.14	2.58	2.18	1.88
72.5	7.3	9.42	7.96	6.82	5.19	4.12	3.38	3.09	2.52	2.12	1.82
67.5	5.9	9.49	7.99	6.82	5.15	4.06	3.30	3.01	2.44	2.04	1.74
62.5	4.7	9.54	7.99	6.80	5.10	4.00	3.23	2.94	2.37	1.97	1.66
57.5	3.7	9.58	7.98	6.75	5.01	3.88	3.11	2.81	2.25	1.84	1.55
52.5	2.8	9.60	7.95	6.68	4.90	3.75	2.98	2.68	2.11	1.71	1.42
47.5	2.1	9.61	7.91	6.61	4.81	3.65	2.87	2.58	2.01	1.62	1.33
42.5	1.5	9.60	7.90	6.59	4.78	3.62	2.84	2.54	1.98	1.59	1.31
37.5	1.0	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30
32.5	0.7	9.60	7.89	6.59	4.77	3.61	2.83	2.53	1.97	1.58	1.30

the examination of hard parts, are extremely difficult and not easily interpreted for tropical species such as the yellowfin tuna.

The marked increase in estimates of size-specific *F* beyond 130 cm for the purse seine gears is a possible result of underestimating ages of older yellowfin. To examine this possibility, the growth curve of LeGuen and Sakagawa (1973) was modified. It was hypothetically assumed that the percentage of underestimation of the time interval within a size interval increased linearly from 0% at 135 cm to 100% at 180 cm. The resulting growth curve is compared to the original in Figure 14.

Values of size-specific *F* were then estimated as before with initial values of 0.2 and 0.8. The value of 0.2 gave the most reasonable results for reasons similar to those given before. Values of size specific *F* for each gear are shown in

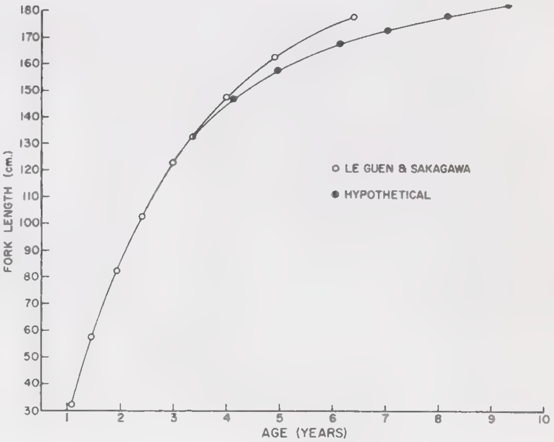

FIGURE 14.—Growth curves of Atlantic yellowfin tuna. Upper curve is from LeGuen and Sakagawa (1973). Lower curve is a modification of the upper curve (see text).

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

BAIT BOATS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	48.87	47.71	46.73	45.18	44.03	43.14	42.78	42.01	41.41	40.91
117.5	30.6	45.55	44.47	43.56	42.12	41.06	40.24	39.90	39.19	38.61	38.14
112.5	26.9	41.63	40.64	39.80	38.47	37.49	36.72	36.40	35.71	35.15	34.68
107.5	23.5	38.03	37.10	36.32	35.08	34.15	33.42	33.10	32.43	31.87	31.40
102.5	20.4	34.67	33.80	33.07	31.91	31.02	30.31	30.01	29.35	28.79	28.31
97.5	17.6	31.19	30.39	29.71	28.63	27.80	27.12	26.83	26.19	25.65	25.19
92.5	15.0	28.34	27.59	26.96	25.95	25.16	24.53	24.25	23.64	23.12	22.67
87.5	12.7	26.21	25.51	24.91	23.95	23.19	22.58	22.31	21.72	21.21	20.77
82.5	10.7	23.80	23.13	22.57	21.65	20.93	20.34	20.08	19.50	19.00	18.57
77.5	8.9	21.12	20.51	19.98	19.12	18.44	17.87	17.62	17.06	16.58	16.16
72.5	7.3	18.89	18.31	17.82	17.00	16.35	15.81	15.57	15.03	14.56	14.16
67.5	5.9	16.57	16.04	15.58	14.81	14.20	13.68	13.45	12.93	12.48	12.09
62.5	4.7	15.08	14.57	14.13	13.39	12.80	12.29	12.07	11.57	11.13	10.75
57.5	3.7	13.31	12.82	12.40	11.70	11.13	10.64	10.42	9.93	9.50	9.13
52.5	2.8	11.97	11.50	11.10	10.41	9.85	9.37	9.16	8.67	8.25	7.88
47.5	2.1	10.87	10.42	10.02	9.35	8.80	8.33	8.11	7.63	7.21	6.85
42.5	1.5	10.57	10.13	9.73	9.07	8.51	8.04	7.83	7.35	6.93	6.56
37.5	1.0	10.51	10.07	9.67	9.01	8.46	7.98	7.77	7.29	6.87	6.50
32.5	0.7	10.51	10.06	9.67	9.00	8.45	7.98	7.76	7.28	6.86	6.50

SMALL PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.08	60.94	58.99	55.67	53.02	50.93	50.04	48.20	46.76	45.59
117.5	30.6	60.95	58.69	56.65	53.18	50.44	48.28	47.36	45.47	43.98	42.78
112.5	26.9	58.62	56.24	54.09	50.47	47.62	45.38	44.44	42.48	40.94	39.69
107.5	23.5	54.53	51.97	49.68	45.87	42.91	40.61	39.65	37.65	36.10	34.85
102.5	20.4	50.69	48.01	45.65	41.78	38.82	36.55	35.61	33.67	32.18	31.00
97.5	17.6	48.15	45.42	43.03	39.15	36.22	33.99	33.07	31.19	29.74	28.60
92.5	15.0	46.71	43.96	41.55	37.66	34.74	32.53	31.61	29.75	28.32	27.19
87.5	12.7	44.78	41.99	39.57	35.67	32.76	30.55	29.64	27.79	26.37	25.24
82.5	10.7	42.99	40.17	37.73	33.82	30.92	28.72	27.82	25.97	24.55	23.43
77.5	8.9	41.01	38.17	35.71	31.79	28.89	26.71	25.81	23.97	22.55	21.41
72.5	7.3	39.22	36.35	33.88	29.96	27.07	24.89	24.00	22.16	20.74	19.60
67.5	5.9	37.02	34.12	31.65	27.73	24.86	22.69	21.80	19.97	18.55	17.41
62.5	4.7	35.35	32.44	29.96	26.06	23.20	21.05	20.16	18.34	16.93	15.79
57.5	3.7	31.69	28.79	26.34	22.51	19.73	17.65	16.79	15.04	13.68	12.59
52.5	2.8	27.97	25.13	22.75	19.09	16.46	14.52	13.72	12.10	10.86	9.88
47.5	2.1	26.14	23.35	21.02	17.47	14.93	13.07	12.31	10.77	9.60	8.67
42.5	1.5	25.72	22.94	20.63	17.10	14.59	12.74	11.99	10.47	9.31	8.39
37.5	1.0	25.62	22.84	20.54	17.01	14.50	12.66	11.91	10.39	9.23	8.32
32.5	0.7	25.61	22.84	20.53	17.00	14.50	12.65	11.90	10.39	9.23	8.32

LARGE PURSE SEINERS

MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	63.26	61.49	59.84	56.92	54.48	52.45	51.57	49.68	48.15	46.90
117.5	30.6	61.30	59.40	57.62	54.49	51.88	49.72	48.78	46.77	45.16	43.83
112.5	26.9	58.69	56.61	54.69	51.30	48.50	46.19	45.19	43.07	41.37	39.98
107.5	23.5	55.99	53.75	51.68	48.07	45.11	42.70	41.66	39.47	37.72	36.31
102.5	20.4	54.78	52.46	50.33	46.62	43.59	41.13	40.07	37.84	36.07	34.63
97.5	17.6	53.40	51.00	48.79	44.96	41.84	39.30	38.21	35.92	34.10	32.62
92.5	15.0	52.39	49.92	47.65	43.73	40.53	37.94	36.83	34.48	32.62	31.10
87.5	12.7	51.41	48.87	46.54	42.52	39.24	36.59	35.45	33.05	31.13	29.57
82.5	10.7	50.10	47.48	45.07	40.91	37.54	34.80	33.63	31.15	29.16	27.54
77.5	8.9	48.65	45.92	43.43	39.13	35.64	32.82	31.61	29.05	27.00	25.32
72.5	7.3	46.62	43.77	41.16	36.69	33.07	30.15	28.90	26.27	24.16	22.45
67.5	5.9	44.46	41.48	38.78	34.14	30.43	27.44	26.17	23.50	21.38	19.66
62.5	4.7	41.92	38.81	36.01	31.24	27.46	24.46	23.18	20.53	18.44	16.77
57.5	3.7	38.35	35.12	32.23	27.39	23.62	20.67	19.44	16.90	14.94	13.40
52.5	2.8	34.39	31.08	28.17	23.39	19.74	16.96	15.82	13.50	11.75	10.41
47.5	2.1	32.91	29.60	26.69	21.96	18.39	15.68	14.58	12.35	10.69	9.42
42.5	1.5	31.85	28.53	25.64	20.94	17.43	14.78	13.70	11.54	9.93	8.71
37.5	1.0	31.52	28.21	25.31	20.63	17.13	14.50	13.43	11.29	9.70	8.49
32.5	0.7	31.52	28.20	25.31	20.62	17.13	14.50	13.43	11.29	9.70	8.49

TABLE 6.—Estimates of average weight of catch (kg) when $M = 0.8$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.—Continued.

					LONG LINERS						
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	59.30	57.92	56.63	54.33	52.38	50.73	50.00	48.41	47.10	46.00
117.5	30.6	57.53	56.05	54.68	52.23	50.16	48.41	47.63	45.96	44.57	43.41
112.5	26.9	55.76	54.18	52.71	50.11	47.91	46.05	45.23	43.45	41.97	40.74
107.5	23.5	54.18	52.51	50.96	48.20	45.87	43.90	43.03	41.14	39.58	38.26
102.5	20.4	52.88	51.13	49.50	46.61	44.16	42.09	41.18	39.19	37.53	36.13
97.5	17.6	52.31	50.51	48.85	45.89	43.38	41.25	40.31	38.26	36.55	35.11
92.5	15.0	51.85	50.02	48.32	45.30	42.74	40.56	39.60	37.49	35.72	34.23
87.5	12.7	51.33	49.46	47.72	44.62	41.98	39.74	38.74	36.55	34.71	33.14
82.5	10.7	50.84	48.93	47.15	43.98	41.27	38.95	37.92	35.65	33.73	32.09
77.5	8.9	50.61	48.68	46.88	43.66	40.91	38.56	37.50	35.19	33.22	31.54
72.5	7.3	50.39	48.44	46.61	43.35	40.56	38.16	37.09	34.72	32.70	30.96
67.5	5.9	50.30	48.34	46.51	43.23	40.41	38.00	36.91	34.52	32.47	30.70
62.5	4.7	50.28	48.31	46.48	43.19	40.37	37.94	36.86	34.45	32.40	30.62
57.5	3.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
52.5	2.8	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
47.5	2.1	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
42.5	1.5	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
37.5	1.0	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56
32.5	0.7	50.26	48.29	46.45	43.16	40.34	37.91	36.82	34.40	32.34	30.56

Figure 15. The values of F of large fish are relatively smaller than those estimated with the original growth curve.

Results of the yield-per-recruit calculations are shown in Table 7. The results indicate that if effort is held constant and size at recruitment is increased to the optimum, less than a 3% increase in yield per recruit would occur. If size at recruitment is constant and effort is doubled, yield per recruit would increase by about 28% which is considerably more than when the original growth curve is used. If size at recruitment is increased to 77.5 cm and effort doubled, a 44% increase in yield per recruit would occur.

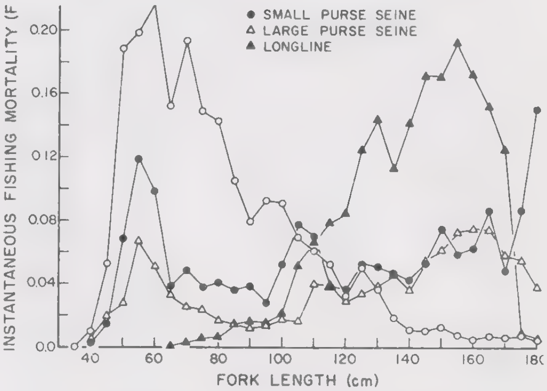

FIGURE 15.—Estimates of size-specific F when its initial value is 0.2 and using the modified growth curve.

TABLE 7.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.8$, initial $F = 0.2$, and hypothetical growth curve is used.

					ENTIRE FISHERY						
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.80	1.48	2.06	2.99	3.70	4.24	4.47	4.95	5.32	5.61
117.5	30.6	0.84	1.55	2.15	3.12	3.85	4.41	4.65	5.13	5.50	5.79
112.5	26.9	0.88	1.62	2.25	3.25	4.00	4.58	4.82	5.30	5.67	5.97
107.5	23.5	0.92	1.70	2.35	3.39	4.15	4.74	4.98	5.46	5.83	6.11
102.5	20.4	0.96	1.76	2.43	3.49	4.27	4.85	5.09	5.57	5.93	6.21
97.5	17.6	0.98	1.80	2.49	3.56	4.35	4.93	5.17	5.64	5.99	6.25
92.5	15.0	1.00	1.84	2.53	3.62	4.40	4.98	5.21	5.68	6.01	6.26
87.5	12.7	1.02	1.87	2.57	3.66	4.44	5.01	5.24	5.69	6.01	6.25
82.5	10.7	1.04	1.89	2.60	3.69	4.47	5.03	5.25	5.69	5.99	6.21
77.5	8.9	1.05	1.92	2.63	3.72	4.48	5.03	5.24	5.65	5.93	6.12
72.5	7.3	1.07	1.94	2.66	3.74	4.48	5.01	5.21	5.59	5.84	6.01
67.5	5.9	1.08	1.96	2.68	3.74	4.47	4.96	5.15	5.49	5.70	5.83
62.5	4.7	1.09	1.98	2.69	3.74	4.44	4.91	5.08	5.39	5.57	5.66
57.5	3.7	1.11	1.99	2.69	3.71	4.37	4.80	4.95	5.20	5.32	5.37
52.5	2.8	1.11	1.99	2.69	3.67	4.28	4.66	4.79	4.98	5.05	5.05
47.5	2.1	1.12	1.99	2.68	3.63	4.21	4.55	4.66	4.81	4.84	4.81
42.5	1.5	1.12	1.99	2.67	3.62	4.18	4.51	4.61	4.75	4.77	4.73
37.5	1.0	1.12	1.99	2.67	3.61	4.18	4.50	4.60	4.73	4.75	4.71
32.5	0.7	1.12	1.99	2.67	3.61	4.17	4.50	4.60	4.73	4.75	4.70

Sensitivity of Results to Errors in Estimates of Natural Mortality

Size-specific values of F were estimated using values of M of 0.6 and 1.0 and an initial value of $F = 0.2$. The results are compared to size-specific F when $M = 0.8$ in Figure 16. Although the absolute values differ considerably, the same general trends appear in each curve. The ratio of F/M varies about threefold.

Results of yield-per-recruit calculations are shown in Tables 8 and 9 and Figures 17 and 18. There is a steeper horizontal gradient when $M = 1.0$ and a steeper vertical gradient when $M = 0.6$ than when $M = 0.8$. That is, yield per recruit is more sensitive to changes in effort

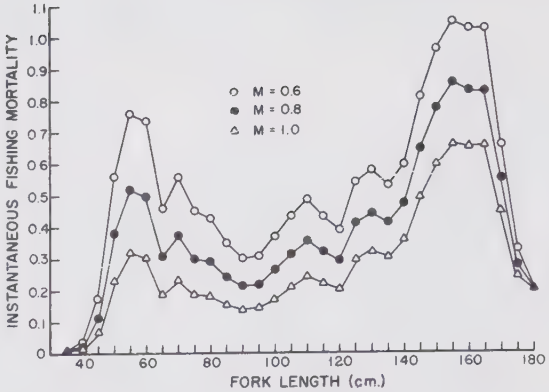

FIGURE 16.—Estimates of size-specific F when its initial value is 0.2 and using values for M of 0.6, 0.8, and 1.0.

TABLE 8.—Estimates of yield per recruit (kg) for the entire fishery when $M = 0.6$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	3.52	5.82	7.34	9.07	9.93	10.39	10.55	10.81	10.98	11.10
117.5	30.6	3.61	5.94	7.47	9.18	10.00	10.43	10.58	10.81	10.95	11.04
112.5	26.9	3.70	6.06	7.58	9.26	10.04	10.44	10.56	10.76	10.86	10.92
107.5	23.5	3.79	6.16	7.68	9.30	10.03	10.38	10.48	10.63	10.70	10.72
102.5	20.4	3.85	6.24	7.74	9.31	9.98	10.28	10.36	10.47	10.49	10.48
97.5	17.6	3.90	6.28	7.77	9.28	9.91	10.16	10.22	10.28	10.27	10.22
92.5	15.0	3.93	6.31	7.77	9.24	9.82	10.03	10.07	10.09	10.04	9.97
87.5	12.7	3.95	6.33	7.77	9.18	9.70	9.87	9.90	9.87	9.79	9.68
82.5	10.7	3.97	6.33	7.74	9.09	9.55	9.66	9.66	9.58	9.45	9.31
77.5	8.9	3.99	6.33	7.70	8.95	9.33	9.38	9.35	9.20	9.01	8.82
72.5	7.3	4.00	6.31	7.63	8.79	9.08	9.06	8.99	8.78	8.54	8.30
67.5	5.9	4.01	6.27	7.53	8.57	8.75	8.64	8.54	8.25	7.94	7.65
62.5	4.7	4.01	6.23	7.44	8.37	8.47	8.29	8.16	7.80	7.45	7.13
57.5	3.7	4.00	6.15	7.28	8.05	8.01	7.73	7.55	7.11	6.70	6.33
52.5	2.8	3.98	6.06	7.10	7.70	7.54	7.16	6.95	6.43	5.97	5.56
47.5	2.1	3.96	5.99	6.96	7.45	7.20	6.75	6.52	5.95	5.46	5.04
42.5	1.5	3.95	5.96	6.92	7.37	7.09	6.62	6.38	5.80	5.30	4.87
37.5	1.0	3.95	5.96	6.90	7.35	7.06	6.59	6.35	5.77	5.26	4.83
32.5	0.7	3.95	5.96	6.90	7.34	7.06	6.59	6.34	5.76	5.26	4.83

TABLE 9.—Estimates of yield per recruit (kg) for the entire fishery when $M = 1.0$, initial $F = 0.2$, and growth curve of LeGuen and Sakagawa (1973) is used.

		ENTIRE FISHERY									
MINIMUM SIZE		MULTIPLIER OF EFFORT									
CM	KG	0.2	0.4	0.6	1.0	1.4	1.8	2.0	2.5	3.0	3.5
122.5	34.6	0.66	1.18	1.62	2.26	2.72	3.06	3.19	3.47	3.67	3.84
117.5	30.6	0.69	1.24	1.68	2.36	2.83	3.18	3.32	3.60	3.81	3.98
112.5	26.9	0.72	1.29	1.76	2.45	2.94	3.30	3.45	3.74	3.96	4.13
107.5	23.5	0.75	1.35	1.83	2.55	3.06	3.42	3.57	3.87	4.09	4.27
102.5	20.4	0.77	1.39	1.89	2.63	3.15	3.52	3.67	3.97	4.20	4.37
97.5	17.6	0.79	1.43	1.93	2.69	3.21	3.59	3.74	4.04	4.27	4.44
92.5	15.0	0.81	1.45	1.97	2.73	3.26	3.64	3.79	4.09	4.31	4.48
87.5	12.7	0.82	1.47	1.99	2.76	3.29	3.67	3.82	4.12	4.34	4.50
82.5	10.7	0.83	1.49	2.02	2.79	3.32	3.70	3.85	4.14	4.35	4.51
77.5	8.9	0.85	1.51	2.05	2.82	3.35	3.72	3.86	4.14	4.34	4.49
72.5	7.3	0.86	1.53	2.07	2.84	3.36	3.72	3.86	4.13	4.32	4.45
67.5	5.9	0.87	1.55	2.09	2.86	3.37	3.72	3.85	4.10	4.27	4.38
62.5	4.7	0.88	1.56	2.10	2.86	3.36	3.70	3.82	4.06	4.21	4.31
57.5	3.7	0.89	1.57	2.11	2.86	3.34	3.65	3.76	3.97	4.09	4.16
52.5	2.8	0.90	1.58	2.11	2.84	3.30	3.58	3.68	3.85	3.94	3.99
47.5	2.1	0.90	1.58	2.11	2.82	3.26	3.52	3.61	3.76	3.83	3.85
42.5	1.5	0.90	1.58	2.10	2.81	3.24	3.50	3.59	3.73	3.79	3.80
37.5	1.0	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79
32.5	0.7	0.90	1.58	2.10	2.81	3.24	3.50	3.58	3.72	3.78	3.79

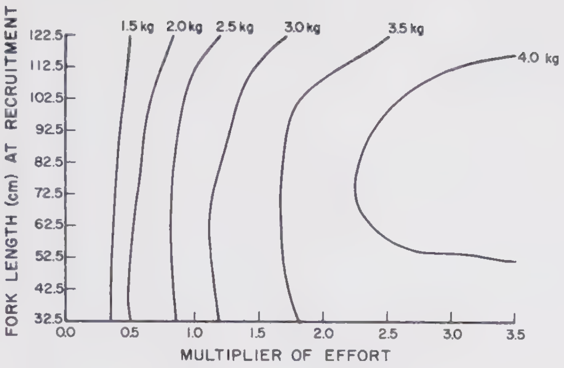

FIGURE 17.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 1.0$.

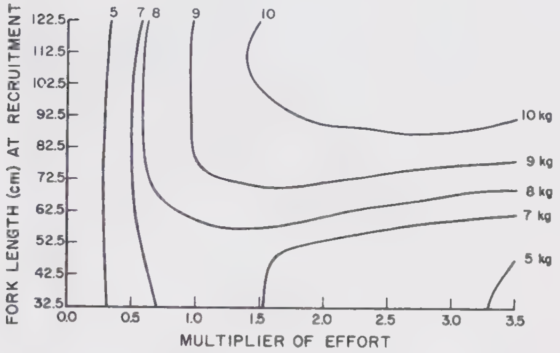

FIGURE 18.—Yield-per-recruit isopleths for the entire Atlantic yellowfin tuna fishery with $M = 0.6$.

when $M = 1.0$ and more sensitive to changes in size at recruitment when $M = 0.6$ than when $M = 0.8$. When $M = 1.0$ and effort is constant an increase in size at recruitment to 77.5 cm does not change yield per recruit. However, when $M = 0.6$, the same change in size at recruitment causes a 22% increase in yield per recruit. When $M = 1.0$ and size at recruitment is held constant, a doubling of effort causes a 29% increase in yield per recruit. When $M = 0.6$, the same change causes a 14% decrease in yield per recruit. When $M = 1.0$ and size at recruitment is increased to 77.5 cm, a doubling of effort causes a 39% increase in yield per recruit. When $M = 0.6$, the same changes cause a 27% increase in yield per recruit.

DISCUSSION

The use of results of our study must be based on three further assumptions: (1) the composition of the fleet will not change; (2) either the gear is currently dispersed so that all qualitative characteristics of the population are available to capture by each gear, or that the dispersal of gear as it now stands will not change; and (3) recruitment is constant.

Relation Between Composition of Fleet and Optimum Size at Recruitment

The preceding text has assumed that the composition of the fleet remains constant. The history of the fishery reveals that the composition has been a very dynamic process and there is no reason to believe that it will not continue to be. Since each fishing gear has a different curve of size-specific F, changes in the fleet composition will cause changes in size-specific F for the entire fleet. These changes will cause changes in the yield-per-recruit isopleths.

To illustrate the influence of changes in fleet composition on management strategy, the optimum size at recruitment was estimated for 441 combinations of baitboat and longline effort. For simplicity, effort of purse seiners is not included, i.e., we excluded two variables—small and large purse seiners. Multipliers of effort for each gear ranged from 0 to 2.0 with increments of 0.1.

The results (Table 10) show a considerable range in the estimates of optimum size at recruitment and that minimum size regulations must be adjusted to changes in the composition of the fleet to maintain maximum yield per recruit. As an example, with a 1.0 level of effort by both gears, the minimum size should be about 72.5 cm. If this were instituted as a minimum size regulation, the bait boat effort might decline to about 0.2 because of the extreme loss of catch. The minimum size, therefore, should be lowered to 67.5 cm. Now the longline effort might increase by about 80% due to the decrease in competition from bait boats—the minimum size should be increased to 77.5 cm. Finally, suppose an innovation occurs in bait fishing such that non-nominal effort again increases to about 0.7—the minimum size should be raised further to about 82.5 cm. These changes could occur slowly allowing for a smooth transition of the minimum size regulations. When economics are involved, however, the changes might be precipitous causing the confusion in the above example. If the possible changes in

TABLE 10.—Optimum size (cm) at recruitment for 441 combinations of multipliers of effort by bait boats and longliners.

Longline multiplier	Bait boat multiplier																				
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
0	32.5	32.5	32.5	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5
0.1	32.5	32.5	32.5	37.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5
0.2	32.5	37.5	42.5	42.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5
0.3	32.5	42.5	47.5	47.5	47.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5
0.4	32.5	47.5	52.5	52.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5
0.5	32.5	52.5	52.5	52.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5
0.6	32.5	57.5	57.5	57.5	57.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.7	32.5	57.5	57.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5
0.8	62.5	62.5	62.5	62.5	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5
0.9	62.5	62.5	62.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.0	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5
1.1	67.5	67.5	67.5	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5
1.2	67.5	67.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.3	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.4	72.5	72.5	72.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5
1.5	72.5	72.5	72.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5
1.6	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5
1.7	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.8	77.5	77.5	77.5	77.5	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
1.9	77.5	77.5	77.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5
2.0	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5	82.5

composition of both small and large purse seiners are included, the attempts to achieve some reason in the minimum size regulation based on maximum yield per recruit can become quite unwieldly.

Dispersion of Gear and Yield Per Recruit

The second assumption could be important. For example, in the eastern Pacific yellowfin tuna fishery effort has expanded farther offshore. Evidence suggests that larger fish were farther offshore and were not previously fully available to the fishery. A possible consequence of this phenomenon is a change in yield per recruit. Upon analysis of the data, the Inter-American Tropical Tuna Commission concluded, however, that the possible increase is minor (Joseph, pers. commun.). The surface gears have been fishing quite close to shore in the Atlantic. The possibility of offshore dispersal of the surface fleets and the effects of such a change on yield per recruit are unknown.

Interaction Between Minimum Size and Catch Quota Regulations

If recruitment is not constant, then the interaction between minimum size and catch quota regulations should be examined. Catch quotas are frequently based on assessments of the maximum sustainable average yield (MSAY), usually through a production model type analysis. The shape of the total yield curve, however, may be strongly dependent on the age at recruitment, t_r'. Therefore, the interaction between the two types of regulation should be examined before a singular action is taken. As an illustration, consider a population consisting of six age-groups with the growth curve and natural mortality coefficient ($M = 0.8$) similar to that of the Atlantic yellowfin tuna fishery, and assume also that recruitment is knife-edged at 19 mo. Figure 19 (lower curve) shows the total annual yield as a function of fishing mortality with an assumed arbitrary stock-recruitment function. Assume further that the fishery is operating at an $F = 1.0$. The yield per recruit at $F = 1.0$ and $t_r' = 19$ mo is 5.39, but the maximum yield per recruit is 6.11 at $t_r' = 27$ mo. If singular action were taken to increase t_r' to 27 mo, the upper total yield curve in Figure 19 would result. Not only did the yield per recruit increase, but so did the total yield at $F = 1.0$. In addition, the MSAY increased, but occurs at a much higher value for F. A phenomenon such as this may have occurred inadvertantly in the eastern tropical Pacific with the introduction of purse seiners which gave a better yield per recruit than the existing bait boats (Joseph, 1970).

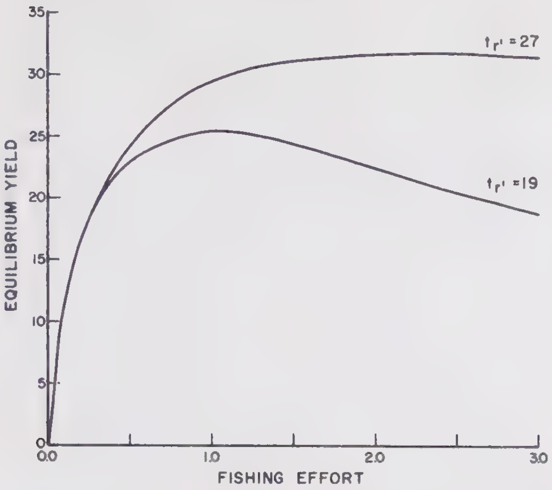

FIGURE 19.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment, t_r'.

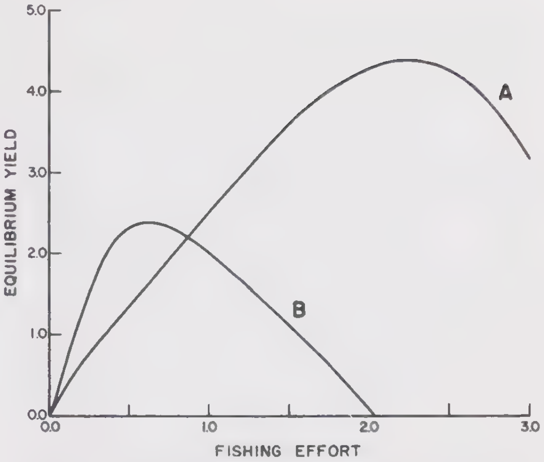

FIGURE 20.—Annual equilibrium yield as a function of fishing effort at two different ages at recruitment (see text).

The above result of singular action on the minimum size regulation resulted in a fortuitous increase in total yield and MSAY. This result may not always occur, however. Consider that if the fishery were operating with t_r' at 27 mo and $F = 0.2$, then the yield per recruit would be 2.77. The optimal yield per recruit is 3.02 at a t_r' of 19 mo. If singular action were taken to lower the t_r' to 19 mo, a slight loss of total yield would occur even with the improved yield per recruit. Even more disconcerting would be the loss in potential MSAY of 28%. The fishery would be suboptimized in a sense. Since the MSAY is usually estimated from a time series of catch and effort data, the actual potential which could have been realized had t_r' remained at 27 mo would likely be underestimated. It is likely that yield per recruit studies would continue as the fishery developed effort beyond $F = 0.2$, such that eventually the upper curve might be attained; this is because the optimal age at recruitment increases asymptotically as F increases. The low initial forecasts of MSAY, however, could hamper development of the fishery.

An even worse consequence of singular action on yield per recruit is illustrated in Figure 20. Assume the fishery is operating at about 0.6 unit of effort with an age at recruitment such to obtain curve A, but the yield per recruit is adjusted to maximal for the age at recruitment giving curve B. The actual MSAY of curve A might never be realized since the maximum equilibrium yield in curve B is also at 0.6 unit of fishing effort. This case represents true suboptimization.

CONCLUSIONS

Although there are some uncertainties in our knowledge of the parameters that enter into calculations of yield per recruit of yellowfin in the Atlantic, it is possible to come to some conclusions from our results.

The least amount of data and assumptions is involved in the simplified Beverton and Holt method. Results from this method (Table 1) show that, in all but a few extreme cases in a wide range of growth and mortality parameter values, an increase in the effective minimum size would result in an increase in yield per recruit. However, our most reasonable estimates of the parameters indicated that at the current level of fishing, an increase in the effective minimum size could only result in about an 8% increase in yield per recruit. We conclude that even if the quality of our data is poor an increase, probably minor, in yield per recruit of Atlantic yellowfin would occur if the effective minimum size is increased and if it is assumed that small yellowfin tuna were not dumped.

We next assumed that our most reasonable estimate of growth, constant Z, and effective minimum size are correct and constructed yield-per-recruit isopleths with the Ricker method for several values of natural mortality. The results (Figures 1-3) indicated that yield per recruit would increase from 0 to 20% if effective minimum size is increased and effort remains constant. Again, our most reasonable estimate of the increase is only 8%. The results also indicate that little if any increase in yield per recruit would occur if fishing effort is doubled and effective minimum size is unchanged. However, if the effective minimum size is increased and effort is doubled, a modest (20 to 40%) increase in yield per recruit could occur. All these results again assume that there would be no dumping of small yellowfin tuna.

We finally assumed that the available data are accurate enough to also make reasonably accurate estimates of size-specific *F*. When using our most reasonable parameter estimates and holding effort constant, an increase in size at recruitment to 55 cm (3.2 kg) would obtain a 3.9% increase in yield per recruit and to 77.5 cm (8.9 kg) would cause less than a 10% increase in yield per recruit. Increasing the size at recruitment to 55 cm with $M = 0.6$ would cause a 7% increase in yield per recruit, but with $M = 1.0$ only a 1% increase would occur. Increasing the size at recruitment to 77.5 cm with $M = 0.6$ would increase yield per recruit by 22%, but with $M = 1.0$ no increase would occur. When size at recruitment is held constant and fishing effort is doubled, our best estimate of the change in yield per recruit is a 6% increase. Our estimates ranged from a 14% decrease to a 29% increase. It seems safe to agree with the report of the Abidjan meeting that if conditions remain constant, there is little to be gained on a yield-per-recruit basis from increases in fishing effort. With a doubling of fishing effort and an increase in size of recruitment to 55 cm, our most reasonable estimate is a 15% increase in yield per recruit, with a range of a 1% decrease to a 35% increase. When size at recruitment is increased to 77.5 cm and fishing effort is doubled, our most reasonable estimate of the change in yield per recruit is a 30% gain; however, the estimates range from 27 to 44%. Thus it appears that if it is possible to increase the size at recruitment, a doubling of effort would produce a modest increase in yield per recruit. These results, it must be noted, assume that small yellowfin tuna are not dumped.

It is interesting to note that the same general conclusions would be made using either the knife-edged recruitment or size-specific *F* approaches. The size-specific *F* approach, in addition, allows us to examine more precisely the effects of an absolute minimum size regulation and the effects on each gear. The general conclusions from both aspects of this study also agree fairly well with those of Joseph and Tomlinson (1972, see footnote 4). It is not surprising, however, that results from the size-specific *F* approach agree with theirs because they used similar methodology and data. Both estimates suggest that under present conditions the fishery is near the point of maximum yield per recruit.

Specifically addressing the recommendations outlined in the introduction section of this paper for considering a minimum size between 3.2 and 10 kg, we offer the following results based on our most reasonable parameter estimates:

1. Minimum size limit 55 cm (3.2 kg):
    a) Current levels of fishing mortality:
        i) No dumping results in a 4% increase in landed yield per recruit
        ii) 100% dumping results in a 3% decrease in landed yield per recruit
    b) Doubling fishing mortality:
        i) No dumping results in a 15% increase in landed yield per recruit
        ii) 100% dumping results in a 1% increase in landed yield per recruit

2. Minimum size limit 77.5 cm (8.9 kg):
    a) Current levels of fishing mortality:
        i) No dumping results in a 9% increase in landed yield per recruit
        ii) 100% dumping results in a 13% decrease in landed yield per recruit
    b. Doubling fishing mortality:
        i) No dumping results in a 31% increase in landed yield per recruit
        ii) 100% dumping results in a 16% decrease in landed yield per recruit.

The 55-cm (3.2 kg) minimum size limit would likely be of more benefit to the tuna fishery than the larger minimum size limit of 77.5 cm (8.9 kg) since less dumping would occur. Therefore, there would likely be, on the average, an increase in landed yield per recruit at the current or greater levels of fishing mortality; whereas, if a larger size limit were adopted, there would likely be, on the average, a decrease in landed yield per recruit at current levels of fishing mortality and less of an increase (perhaps even a decrease) in landed yield per recruit than with the 55-cm (3.2 kg) minimum size and an increase in fishing mortality.

The results of this paper were obtained using reasonable assumptions and all available data on Atlantic yellowfin tuna. As we increased the number of assumptions we increased the number of conclusions. We think that it is unlikely that use of tecnhiques not used in this paper would result in conclusions that are significantly different from ours. That is, an increase in effective minimum size would result in a minor increase in yield per recruit, an increase in effort without increasing effective minimum size would not appreciably increase yield per recruit, and an increase in effective minimum size and effort would result in modest gains in yield per recruit. We wish to emphasize that these conclusions are based on a number of assumptions. We consider the assumptions reasonable, but because they are assumptions any management decisions, including the decision of taking no action, should be followed with careful evaluation of the results.

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We are indebted to James Joseph and Patrick Tomlinson of the Inter-American Tropical Tuna Commission for their useful comments on this paper. This study would not have been possible without the many valuable contributions of data and ideas by scientists of the nations that participate in the International Commission for the Conservation of Atlantic Tunas.

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Analysis of Length and Weight Data On Three Species of Billfish From the Western Atlantic Ocean

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ABSTRACT

Estimates of parameters of relations among weight, girth, total length, fork length, body length, trunk length, and caudal spread were made for blue marlin, white marlin, and sailfish captured in the western Atlantic. Some sexual differences were found.

Estimates of relations between length and weight of fish are important, because weight is often the desired measure when only length measurements are practical. For example, obtaining accurate weights on vessels at sea is difficult, especially when specimens may weigh hundreds of pounds, as is often the case for billfish. Both sport and commercial fishermen are more interested in weight than in length, for game fish records are listed by weight and commercial fishermen are paid by the weight of their catch.

Although length measurements of billfish have been taken in numerous ways (Rivas, 1956; Royce, 1957), we chose eye-fork length as the most meaningful, because it involves parts of the body that are least apt to be damaged.

In this study we estimated relations between eye-fork length and weight for blue marlin *(Makaira nigricans),* white marlin *(Tetrapturus albidus),* and sailfish *(Istiophorus platypterus)* in the western Atlantic Ocean. The relations between girth, eye-fork length, and weight were also estimated, for weight can be more accurately estimated from eye-fork length and girth than from eye-fork length alone. The relations between total length, fork length, body length, caudal spread, and eye-fork length were estimated so that measurements of the first four types could be converted to eye-fork length for comparative purposes. We also examined sexual, spatial, and temporal differences among some of the relations.

SOURCES OF DATA AND TYPES OF MEASUREMENTS

Most of the data were obtained by personnel of the Panama City Laboratory, Gulf Coastal Fisheries Center, National Marine Fisheries Service, from sportfishermen's catches in the northeastern Gulf of Mexico during 1971. Weights, lengths, girths, and sex were determined for billfishes landed at Port Eads, Louisiana, and at three ports in northwest Florida: Pensacola, Destin, and Panama City.

Data were also obtained from cooperative scientists for catches made in various years off the coasts of New Jersey, North Carolina, and Florida, around the Bahama Islands, in the Caribbean Sea, and off Rio de Janeiro.

Most measurements were made in English units, a few in metric units. All weights were recorded in pounds. Lengths were recorded in inches or in centimeters. Metric measurements were converted to inches for the analyses, since sportsmen and commercial fishermen use inches and pounds. Four kinds of length measurements plus the girth and caudal spread were made by personnel of the Panama City Laboratory, except when conditions did not permit (e.g., broken bill or shark bites). Data from the cooperating scientists consisted of one or two kinds of length plus weight.

Measurements and their criteria are listed below. Criteria for body length, girth, and caudal spread are the same as those of Rivas (1956). All, except girth, consisted of horizontal, straight-line measurements.

(1) Total length: tip of bill to line joining tips of caudal lobes.

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(2) Fork length: tip of bill to tips of mid-caudal rays.
(3) Body length: tip of lower jaw (with jaws closed) to tips of mid-caudal rays.
(4) Eye-fork length: posterior margin of eye to tips of mid-caudal rays.
(5) Caudal spread: dorsal tip to ventral tip of lobes of caudal fin.
(6) Girth: twice the curved distance along one side of the body from the pelvic groove to the dorsal edge of the dorsal groove.

METHODS OF ANALYSIS

Three equations were used in the study. The relation between $\log_{10}$ (weight) and $\log_{10}$ (eye-fork length) is given by

$$Y = A + B_1 X_1 \tag{1}$$

where

Y = $\log_{10}$ (weight),
A = intercept,
B_1 = coefficient,
X_1 = $\log_{10}$ (eye-fork length).

The equation can be transformed to the familiar form

$$\text{weight} = A' \,(\text{eye-fork length})^{B_1}$$

where

$$A' = 10^A$$

by taking antilogs of both sides of (1). The relation between $\log_{10}$ (weight), $\log_{10}$ (eye-fork length), and $\log_{10}$ (girth) is given by

$$Y = A + B_1 X_1 + B_2 X_2 \tag{2}$$

where

Y = $\log_{10}$ (weight),
A = intercept,
B_1 and B_2 = coefficients,
X_1 = $\log_{10}$ (eye-fork length),
X_2 = $\log_{10}$ (girth).

The equation can be transformed to

$$\text{weight} = A' \,(\text{eye-fork length})^{B_1}\,(\text{girth})^{B_2}$$

by taking the antilogs of both sides. The relations between eye-fork length and other measures of length are given by

$$Y = A + B_1 X_1 \tag{3}$$

where

Y = eye-fork length,
A = intercept,
B_1 = coefficient,
X_1 = other measure of length.

Equation (1) was not used for the relation between the various measures of length because estimates of B were very close to 1, indicating that linear relations among the variables were appropriate. Equation (3) was used instead.

The parameters of (1), (2), and (3) were estimated by use of linear regressions. Analysis of covariance was used to examine sexual differences. Multivariate analysis was used to determine if white marlin could be sexed or allocated to either Florida or Louisiana given measures of length and weight.

RESULTS AND DISCUSSION

Estimates of the parameters of (1), (2), and (3) are shown in Table 1. All estimates of the parameters are significantly different from 0 at the 0.01 level of significance.

Analyses of covariance revealed no significant differences between sexes in the relations between weight and eye-fork length, between eye-fork length and the three other measures of length, and between eye-fork length and caudal spread for blue marlin. However, sexual differences were found in the relations between weight and eye-fork length and between eye-fork length and caudal spread for white marlin (Fig. 1 and 2). Female white marlin tend to weigh more at a given length than male white marlin, but this difference tends to disappear at larger sizes. Further examination of the data indicates that the difference is partially the result of females tending to have deeper bodies than males. Male white marlin tend to have a wider caudal spread than females and the difference tends to increase with size. A sexual difference in caudal spread was also found for sailfish (Fig. 3), but the difference decreases with increased size. Sexual differences were not found in the length-weight relation for sailfish.

Deviations from the length-weight relation of the

Table 1.—Estimates of parameters of equations (1), (2), and (3).

Species	Y^1	X^1_1	X^1_2	A	B_1	B_2	Sample size	Standard error	*Range of X_1* (inches)	
									Minimum	Maximum
Blue marlin	W	LL4	—	-3.84620	3.28222	—	78	0.0566	50.8	103.5
Blue marlin	W	LL4	G	-3.15120	1.80496	1.27853	78	0.0390	50.8	103.5
Blue marlin	L4	L1	—	1.68522	0.66670	—	80	1.9740	73.0	149.0
Blue marlin	L4	L2	—	3.07821	0.72374	—	80	1.6853	64.0	134.0
Blue marlin	L4	L3	—	-0.74597	0.88352	—	83	2.1451	58.0	117.0
Blue marlin	L4	TT	—	4.33691	1.93860	—	75	5.1410	24.0	48.0
White marlin	W	LL4	—	-2.41011	2.37515	—	182	0.0593	47.5	70.0
White marlin	W	LL4	G	-2.20239	1.24968	1.25290	177	0.0472	47.5	70.0
White marlin	L4	L1	—	-0.71780	0.66084	—	196	1.8680	72.5	99.0
White marlin	L4	L2	—	-0.59179	0.73942	—	193	1.5571	65.5	91.0
White marlin	L4	L3	—	1.17904	0.83010	—	192	1.1205	56.0	79.0
White marlin	L4	TT	—	40.38790	0.64258	—	185	3.0604	11.0	27.0
Sailfish	W	LL4	—	-3.89480	3.15757	—	244	0.0532	15.8	62.5
Sailfish	W	LL4	G	-3.36702	2.27782	0.73757	242	0.0480	15.8	62.5
Sailfish	L4	L1	—	-1.96822	0.68216	—	260	1.5403	26.0	93.0
Sailfish	L4	L2	—	-1.09314	0.75088	—	260	1.2235	23.0	85.0
Sailfish	L4	L3	—	-0.78628	0.87262	—	267	0.9175	19.2	72.5
Sailfish	L4	TT	—	11.66889	1.87509	—	256	4.0575	4.0	28.0

[1] W = $\log_{10}$(weight)
LL4 = $\log_{10}$(eye-fork length)
L4 = eye-fork length
L1 = total length
L2 = fork length
L3 = body length
TT = caudal spread
G = girth

three species were plotted against month of capture to examine the possibility of seasonal patterns in the relations. None was found.

Multivariate analysis was used in an attempt to develop a method of sexing white marlin given weight, caudal spread, and the measures of length. Approximately 75% of the specimens could be properly sexed. Although this procedure produced better results than pure guesswork, the results are not satisfactory for scientific purposes.

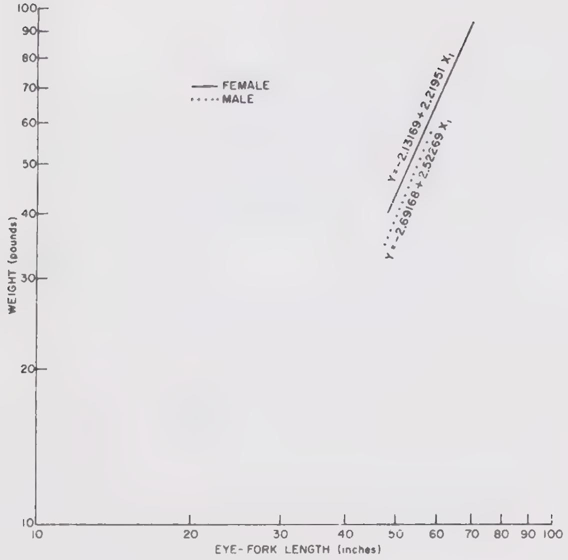

Figure 1.—Relationship of weight and eye-fork length of white marlin *(Tetrapturus albidus)* by sex.

Multivariate analysis was also used to determine if white marlin could be allocated to Florida or Louisiana given weight, caudal spread, and the measures of length. White marlin could not be so allocated.

A review of the literature revealed that very little had been done on length-weight relations of billfishes in the western Atlantic Ocean. De Sylva and Davis (1963) estimated the relation between body length and weight for white marlin and noted the same sexual difference found in this study. De Sylva (1957) plotted weight and total lengths of sailfish but did not estimate the parameters of the relation.

The results of our analyses will permit conversions from one type of length to another and also will provide better estimates of weight from length plus girth measurements.

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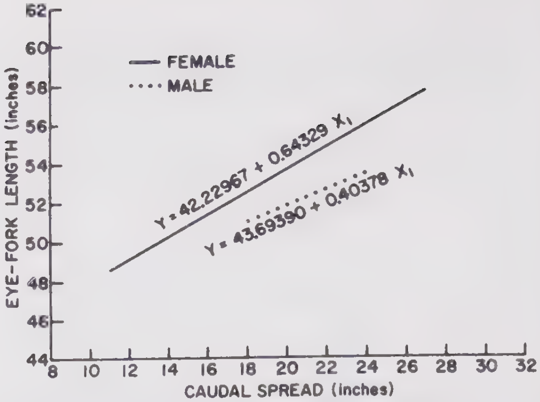

Figure 2.—Relationship of eye-fork length and caudal spread of white marlin *(Tetrapturus albidus)* by sex.

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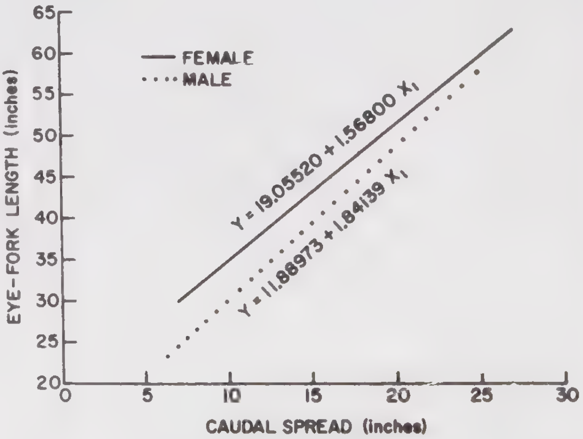

Figure 3.—Relationship of eye-fork length and caudal spread of sailfish *(Istiophorus platypterus)* by sex.

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CHANGES IN THE AMOUNT AND PROPORTIONS OF DDT AND ITS METABOLITES, DDE AND DDD, IN THE MARINE ENVIRONMENT OFF SOUTHERN CALIFORNIA, 1949–72

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ABSTRACT

This paper is about the contamination of the ocean and its biota off southern California by the pesticide, DDT. The accumulation of DDT and the changes in proportions of DDT and its metabolites in the ocean are described for the years 1949 to 1972 especially as they are reflected in the myctophid fish, *Stenobrachius leucopsarus*. This time period was characterized by continuous dumping of DDT wastes into the ocean by a large manufacturer of DDT and the cessation of this dumping in 1970. Aspects and implications of the pesticide pollution problem in the marine environment are discussed.

In January and May 1970, the Fishery–Oceanography Center, La Jolla, Calif., collected samples of fish off southern California and Baja California as their part in a survey of chlorinated hydrocarbon (CHC) pesticides in marine fishes by the U.S. fish and Wildlife Service Bureau of Commercial Fisheries (now the National Marine Fisheries Service). Each sample consisted of the livers of several specimens of a single species from one locality. The samples were sent to the Environmental Protection Agency Laboratory at Gulf Breeze, Fla., for analysis.

The results (Duke and Wilson, 1971) showed that off southern Baja California 9 samples (170 fish) contained an average of 0.14 parts per million (ppm) wet weight of DDT and its metabolites; in Sebastian Vizcaino Bay (central Baja California) 3 samples (29 fish) averaged 1.2 ppm; along the southern California coast south of Oceanside and at two offshore banks 15 samples (179 fish) averaged 13 ppm; in Santa Monica Bay 8 samples (65 fish) averaged 370 ppm. Two samples (26 fish) of Pacific hake, *Merluccius productus,* taken by a Russian trawler off northern California and Oregon averaged 2.7 ppm, and fish sampled farther to the north by the Seattle Laboratory contained less than 1 ppm or no detectable DDT residues in the livers. The highest levels of DDT and its metabolites were found in the Los Angeles area with DDT levels declining greatly in samples taken to the north, south, and offshore from Los Angeles.

Previous pesticide residue surveys of marine birds and fish (Keith and Hunt, 1966; Risebrough et al., 1967; Risebrough et al., 1968) had been confined primarily to central California and did not reveal the extent of DDT pollution in the ocean off Los Angeles. Risebrough et al. (1967) reported one sample of northern anchovy, *Engraulis mordax,* taken off Los Angeles that contained 12.7 ppm DDT and its metabolites compared with additional samples of anchovies and three other species of fish taken north of Los Angeles to San Francisco that ranged in DDT residue content between 0.2 and 2.8 ppm.

In the spring of 1969, Keith, Woods, and Hunt (1970) investigated the breeding pelican, *Pelecanus occidentalis,* colony on Anacapa Island, about 35 nautical miles west of Santa Monica Bay, and found extensive reproductive failure caused by thin–shelled eggs which broke under the brooding pelicans. They found that the contents of a composite sample of many broken eggs contained 1,818 ppm DDT residues (lipid basis) while nine intact eggs averaged 1,215 ppm. They also sampled pelican eggs from three breeding colonies in the Gulf of California and found DDT residues averaging 58, 61, and 105 ppm. Jehl (1970) sampled pelican eggs from Los Coronados Islands, about 95 nautical miles south of Anacapa. These contained 810 ppm DDT residues. At San Martin Island 250 nautical miles south of Anacapa, egg residues were 192 ppm.

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More recent data (Southern California Coastal Water Research Project, 1971)[2] for the *p,p'*DDE content of the mussel, *Mytilus californianus,* show that two samples taken on the Palos Verdes Peninsula, near Los Angeles, contained 61 and 151 ppm of *p,p'*DDE while samples taken at a greater distance from Los Angeles declined greatly to between 0.3 and 3 ppm at San Diego, Point Conception, and on the farther outlying islands.

Burnett (1971) determined DDT residues in samples of the sand crab, *Emerita analoga,* from 19 locations along the coast between northern Baja California and San Francisco. Only in those crabs from the Los Angeles area did he find values greater than 1 ppm (up to 7.2 ppm). The DDT values fell off rapidly north and south of Los Angeles and averaged about 0.1 ppm at most of these locations.

These results of the above studies demonstrate that geographical proximity to Los Angeles was accompanied by greatly elevated levels of DDT and its metabolites in marine organisms.

High DDT residues in marine life in the ocean off Los Angeles had an adverse effect on the fishing industry. In June 1970, canned jack mackerel, *Trachurus symmetricus,* shipped from Los Angeles was condemned by the U.S. Food and Drug Administration in New York for high DDT content (13 ppm). The FDA had set a maximum tolerance of 5 ppm on fish products. In the following year jack mackerel was withheld from distribution by the packers, and jack mackerel and Pacific bonito, *Sarda chiliensis,* were condemned by the FDA in the Los Angeles area. In December 1970, the FDA seized about 8,000 lb of white croaker, also called kingfish, *Genyonemus lineatus,* that had been caught near Los Angeles. These contained 19 ppm DDT residues.

While the fishing industry was unable to pinpoint any particular area of heavy DDT contamination of pelagic fish off southern California, it seemed to be fairly well defined for the more sedentary bottom dwelling species. Although the total DDT in the flesh of the Santa Monica Bay fish samples taken in May 1970 ranged from 12 to 57 ppm, about 30 nautical miles away at Farnsworth Bank on the west side of Santa Catalina Island, DDT in the flesh of a sample of sculpin, *Scorpaena guttata,* and in flesh samples of four species of rockfishes, *Sebastes* spp., had a range of only 0.23 to 0.49 ppm; and, a sample of white croakers taken off Oceanside, 40 nautical miles south of Los Angeles, contained only 0.61 ppm of DDT residues in the flesh.

The pelagic fish were not good indicators of the source of pesticide contamination because they are much more migratory than the bottom dwelling species, and the area in which they are caught is not necessarily the area in which they were contaminated. Even though this would also mean that their exposure to heavy contamination would be of shorter duration than for bottom fishes living in these areas, they still built up high concentrations of DDT in the flesh because pelagic fish tend to store fat throughout the body rather than in the liver as do bottom dwelling, more sedentary species. The DDT residues are stored in the fats, and the distribution of the total body load of DDT residues in the fish is roughly related to the distribution of fat.

Although we have no flesh sample analyses from pelagic fish to illustrate this point, concentrations of DDT were found to be two to six times higher in the livers of samples of four different species of bottom dwelling fish taken in 1970 along the coast between San Diego and Oceanside than they were in the livers of a sample of jack mackerel from the same area, and seven to 19 times higher than in the livers of a sample of Pacific sardine, *Sardinops sagax,* taken in San Diego Bay at about the same time. And even among bottom fish taken from the same area at the same time, those that have more oil in the flesh seem to carry relatively more of the total DDT load in the flesh. For five species of bottom dwelling fishes taken from Santa Monica Bay in 1970, there is an inverse relation between the ratio of DDT in the liver to DDT in the flesh and the percent of oil in the flesh as given in Table 1.

Because of the prevalence of winds from the Pacific, and the concentration of agriculture in the inland valleys, we considered it unlikely that the heavy DDT contamination in the ocean off Los Angeles was caused by airborne pesticide residues. Surface runoff was also an unlikely source. Southern California's arid climate, the damming of rivers, the large population and importation of water have resulted in a condition in which the annual discharge by sewers into the ocean is at least twice the average annual surface runoff of

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[2] Southern California Coastal Water Research Project, 1971. Comments on the policy for water quality control proposed by the State Water Resources Control Board. Presented at the State Water Resources Control Board public hearing, San Diego, Calif., 2 Dec. 1971, 27 p.

TABLE 1.—Relation between ratio of DDT in liver to DDT in flesh and percent of oil in flesh of five species of bottom dwelling fishes from Santa Monica Bay in 1970.

Species	Number of fish	Total DDT Liver (ppm)	Total DDT Flesh (ppm)	Ratio of DDT Liver:flesh	Percent oil in flesh
Bocaccio, *Sebastes paucispinis*	9	590	12	49:1	1.4
Starry rockfish, *S. constellatus*	5	1,030	57	18:1	1.8
Vermilion rockfish, *S. miniatus*	10	163	16	10:1	2.2
Dover sole, *Microstomus pacificus*	13	63	13	5:1	3.6
Sablefish, *Anoplopoma fimbria*	10	103	23	4:1	6.0

water. The "rivers" of southern California are its sewers, and the two largest of these, in the 400 million gallons (1.51 million m^3) per day class, are the outlets of the Hyperion treatment plant that serves the city of Los Angeles and those of the White Point treatment plant that serves Los Angeles County.

The Hyperion plant empties into the head of an underwater canyon in the northern half of Santa Monica Bay, and the White Point plant empties into the ocean off Palos Verdes Peninsula. Fish samples that showed very high DDT residues came from southern Santa Monica Bay about midway between the two sewer outfalls.

The County Sanitation Districts of Los Angeles County (CSDLAC) began a monitoring program to test for CHC pesticides in its sewerage system in December 1969 (Carry and Redner, 1970). They found that very high concentrations of DDT were present in the sewer system. In March 1970, they began to sample the sewer trunk lines in order to pinpoint the sources of DDT input into the sewer system.

They soon discovered that the source of most of the DDT pollution was the Montrose Chemical Corporation, a major manufacturer of DDT, located in the city of Torrance. Los Angeles Times staff writer, John Dreyfus, reported (7 October 1970), after interviewing a Montrose official, that at that time, Montrose was the only manufacturer of DDT left in the United States, and that it accounted for two–thirds of the world's sales of DDT.

The CSDLAC found that water samples taken from the sewers immediately upstream from Montrose contained 34 parts per billion (ppb) of DDT and its metabolites (DDD and DDE) in a flow of 25.3 million gallons (95.8 thousand m^3) per day or 7.2 lb (3.27 kg) of total DDT per day, while samples taken immediately downstream contained 2,950 ppb in a flow of 26.6 million gallons (100.7 m^3) per day or 654 lb (297 kg) of total DDT per day (Carry and Redner, 1970).

In April 1970, Montrose began hauling most of its processing wastes to a storage area, which caused a considerable drop in CHC entering the CSDLAC disposal plant. However, in May 180 lb (81.6 kg) per day CHC, of which 150 lb (68.0 kg) was DDT and its metabolites, were still found to be entering the White Point plant. The primary source of this was found to be the sewer trunk line serving Montrose Chemical Corporation. Because the composition of the total DDT sampled, 14% DDT, 48% DDD, and 38% DDE, was different from the Montrose effluent previously sampled, 74% DDT, 5% DDD, and 21% DDE, CSDLAC personnel concluded that the primary source of pollution was from old deposits in the sewer lines.

Between 11 December 1970, and 1 July 1971, 567,000 lb (257,000 kg) of deposits, of which 7,700 lb (3,500 kg) were total DDT, were removed from the interceptor system that served Montrose (Redner and Payne, 1971). The cleaning of this section of the sewer lines also stirred up old deposits which were washed down into the sewerage disposal plant, resulting in an increase in total DDT entering the plant. By October 1971, the total CHC entering the disposal plant had decreased to 60 lb (27 kg) a day of which 28 lb (13 kg) was total DDT and the remaining 32 lb (14 kg) polychlorinated biphenyls (PCB).

Since March 1971, an average of 22,000 gallons (83.3 m^3) a day of alkaline waste from the Montrose plant has been trucked to the Sanitation District's landfill on Palos Verdes Peninsula, and another 700 gallons (25.9 m^3) of acid waste has been trucked to a quarry. The alkaline waste was found to contain about 3,000 ppm of total DDT (Redner and Payne, 1971) or about 550 lb (250 kg) per day. The acid waste was not tested, but if the concentration of DDT was similar to that in the alkaline waste, it would amount to an additional 175 lb (79 kg) of DDT residues per day.

The average inflow of DDT into the White Point sewerage plant during December 1969 through March 1970 was estimated at 652 lb (296 kg) per day. The amount measured in the sewers at the Montrose plant was 647 (293 kg) per day. The amount trucked out as alkaline waste only was estimated at 550 (250 kg) per day. Considering the difficulties in sampling such large volumes of material and the fact that the samples were taken in different localities at different times, there is remarkable agreement among them.

It is difficult to determine just how much DDT finally was pumped into the ocean after treatment at the sewerage plant. Some of it was undoubtedly removed in grit, grease skimming operations, and in dried sludge.

At the Hyperion treatment plant (city of Los Angeles), the digested sludge is pumped into the ocean, although some of it, at least in the past, has been used for fertilizer. The DDT input into the Hyperion plant was estimated to be on the order of 0.6 lb (0.27 kg) a day (tests by Hyperion personnel cited in Los Angeles Times, 7 October 1970) so, insofar as the DDT input into the ocean is concerned, it has had little impact. The White Point treatment plant has never discharged its sludge into the ocean (Terry Hindrichs, Southern California Coastal Water Research Project, pers. commun.) except during a short period of heavy rains in 1955. Until 1959, digested sludge was spread on nearby fields to air dry. Since 1959 a centrifuge has been used to partially dry sludge. The resulting cakes have been used for fertilizer or landfill.

CSDLAC personnel were unable to get reliable estimates of the DDT content of their effluent into the ocean until December 1970 (Carry and Redner, 1970), long after Montrose stopped dumping most of their wastes. Nine samples that they took from the effluent into the ocean in December showed that the average total CHC entering the ocean was 130 lb (59 kg) a day. The influent into the sewerage disposal plant in December had a load of 153 lb (69 kg) per day. The influent samples were taken after the grit chambers so any CHC removed in grit would not have been included. If we assume that sludge removal accounted for a 15% loss of CHC in December 1969 through March 1970, between influent (average 652 lb or 296 kg per day) and effluent into the ocean, then, the ocean discharge would have been about 552 lb (250 kg) per day of CHC for these months. This is about 100 short tons (91 metric tons) per year or about 10 times the amount of pesticides estimated to be carried into the Gulf of Mexico each year by the Mississippi River (Butler, 1969).

Montrose received a permit to dump its wastes into the CSDLAC sewer system in 1953, but it had been dumping for a few years before that according to company personnel. The continuous dumping of large quantities of DDT wastes into the ocean at a single point over a period of about 20 yr presented an unparalleled opportunity to study the effects of DDT on the ocean environment. Unfortunately the one–time opportunity to take advantage of the situation was not fully realized until some time after the dumping had stopped, and no large–scale coordinated investigation was undertaken to exploit this ecological windfall.

An investigation of pesticide pollution of the marine environment was initiated at the Fishery Oceanography Center (FOC), La Jolla, in 1970. Personnel at FOC have collected samples of bottom muds, fishes, and other biological samples primarily from the ocean off Los Angeles in order to study the effects of heavy DDT pollution in the marine environment.

Collections of marine organisms taken for other purposes, some dating back to 1949, were available for study. Most of the present paper is based on DDT levels found in specimens from one of these collections of a myctophid fish, *Stenobrachius leucopsarus,* found in the ocean off southern California in an attempt to trace the historical buildup of DDT and its metabolites in the marine environment as reflected in this species.

MATERIALS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has taken plankton samples over an extensive area off California and Baja California since 1949. These samples were obtained over a predetermined pattern of stations in order to determine the species present, their numbers, and their distribution. The most intensive sampling took place during the 1950's; during the 1960's the number of CalCOFI cruises was reduced considerably.

All fish and fish eggs are routinely sorted out of the collections for identification. About 600 specimens of the myctophid fish, *S. leucopsarus,* that had been sorted from the plankton collections, were selected for this study to give best areal and temporal coverage.

Initially a few plankton samples, which were available in much greater quantity, were tested for pesticides. However, the plankton species composition varied in time and with locality, and it was felt that the samples might not be comparable. The plankton samples also appeared to contain both Aroclor 1242[3] and Aroclor 1254 (polychlorinated biphenyls (PCB) manufactured by Monsanto Corporation) while the myctophids generally contained only Aroclor 1254 in quantity. Plankton samples can include man-produced debris that contains relatively large amounts of CHC or other organic chemicals which interfere with analysis, while individual myctophids are relatively free of such material. Myctophids do not undergo any more horizontal movement than other plankton organisms, and, if they use their motility at all, at least in the coastal waters, it is probably to maintain position over the deeper basins. In addition, they tend to contain more pesticide than the invertebrate constituents of the plankton with which they are taken, and they are convenient material to work with.

The myctophids tested for pesticide residues ranged in standard length (SL) from 14 to 77 mm. They are apparently short-lived fish. Fish of the year can be followed through their first year and into their second by length-frequency distributions (Figure 1). Most of the myctophids tested appeared to be comparable in DDT content to other fish taken at the same time and place, but the amounts in smaller fish were erratic. Some

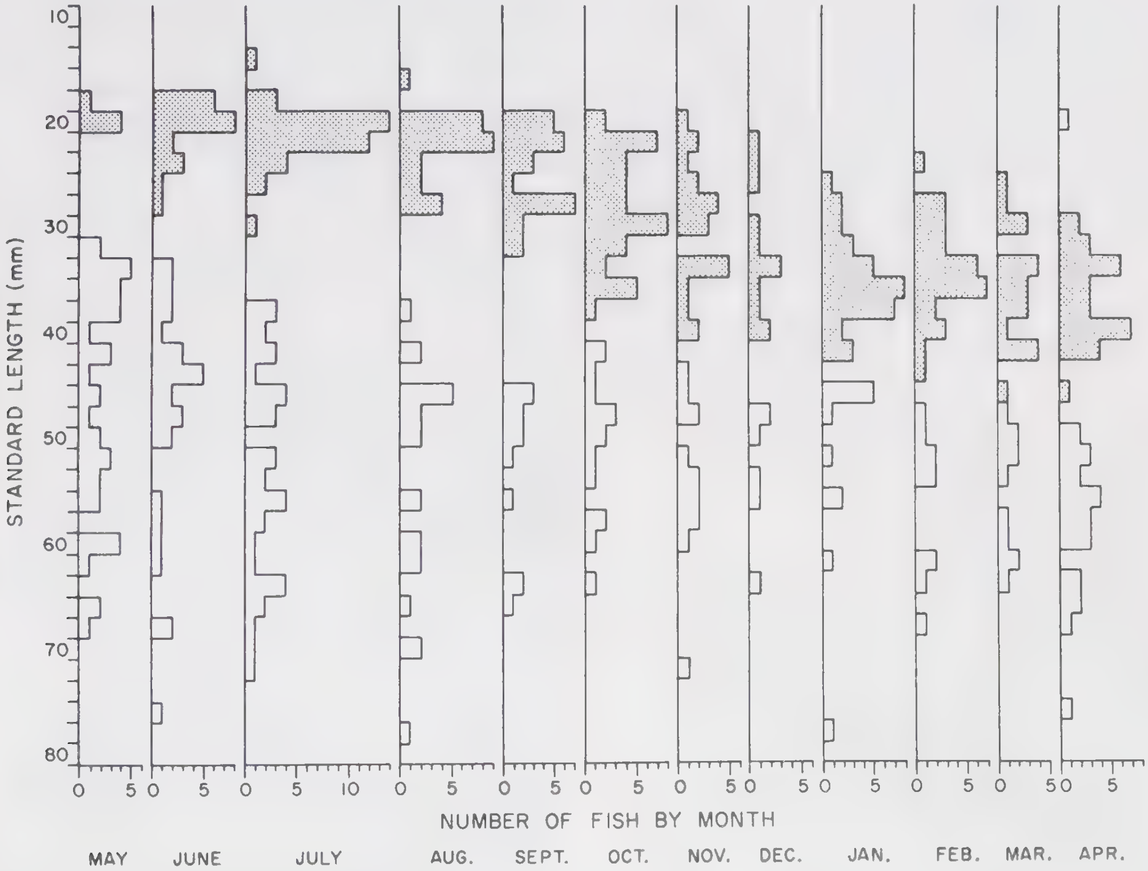

FIGURE 1.—Length-frequency distribution of *Stenobrachius leucopsarus* by month. Shaded area is entering year class.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

were comparable to larger fish, while others contained less DDT than might be expected in larger fish taken at the same time and in the same locality.

This variation in pesticide content appeared to be related to the "fat" content (hexane extractable portion of the fish) of the specimens. The fat content of the fishes (Figure 2) increased very rapidly and with considerable variation to 30 mm length, 6.5% fat of the dry weight of the fish in an 18–mm specimen to 42.5% in a 29–mm specimen) where it began to level off. In mature fish the fat is about 49% of dry weight and 16% of wet weight. There is no apparent seasonal fat cycle. For comparison of DDT in time and space, only myctophids 30 mm or longer were used.

METHODS

The myctophids used in this study were preserved in Formalin which had no apparent effect on the pesticides to be analyzed. The specimens were measured and weighed and placed in tared disposable pipets that had been plugged with glass wool at the small end, or for larger fish in similarly prepared glass tubing of appropriate size. The fish were dried in an oven at 65°C to constant weight and reweighed to obtain dry weight. Each fish was macerated in the tube and extracted into a 15–ml graduated centrifuge tube with 10 ml of hexane. The remains of the fish in the pipet were dried and reweighed to obtain the weight of material extracted.

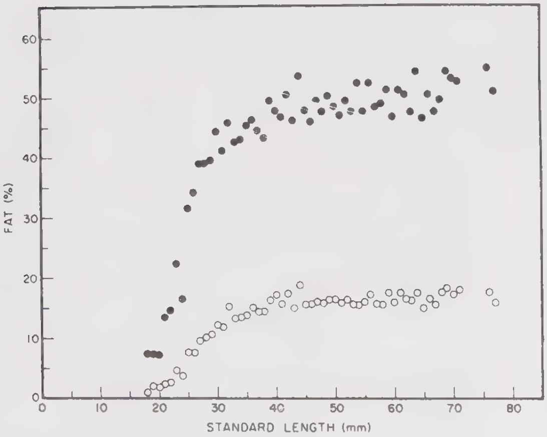


FIGURE 2.—Increase in percent fat with increase in length for *Stenobrachius leucopsarus*. Dark circles equal fat as a percent of dry weight; open circles, as a percent of wet weight. Fat equals hexane extractable substances. Pesticide values for fish less than 30 mm standard length (SL) were not used because of the greater variation in these values than in larger fish in which fat content was more stabilized.

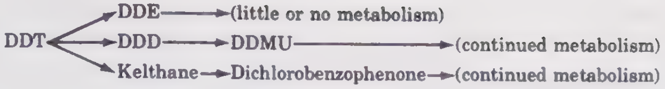
The extract in the centrifuge tube was mixed to uniformity, and an aliquot equal to 20 mg or less of fat removed. This was reduced in volume if necessary and passed through an activated alumina column as described by McClure (1972). The cleaned up sample was again reduced in volume if necessary and injected into a model 402 Hewlett Packard gas chromatograph (GLC) with a Ni^{63} electron capture detector. The 6–foot glass column contained 1.5% OV–17/1.95%QF–1, on 100/120 mesh Supelcoport.

DDT gets its name from its former chemical designation, *p,p'*–dichlorodiphenyltrichloroethane. The current chemical designations for DDT and its metabolic products mentioned in this paper are:

p,p'–DDT	1,1–dichloro–2,2–bis(*p*–chlorophenyl)ethane
p,p'–DDD (TDE)	1,1–dichloro–2,2–bis(*p*–chlorophenyl)ethane
p,p'–DDE	1,1–dichloro–2,2–bis(*p*–chlorophenyl)ethylene
p,p,'–DDMU	1–chloro–2,2–bis(*p*–chlorophenyl)ethylene
Kelthane (Dicofol)	1,1–bis(*p*–chlorophenyl)–2,2,2–trichloroethanol

For the ortho–para isomers of DDT, DDD, DDE, and DDMU substitute 2(*o*–chlorophenyl)–2–(*p*–chlorophenyl) for 2,2–bis(*p*–chlorophenyl). In this paper total DDT includes *p,p'*DDT, *o,p'*DDT, *p,p'*DDD, *o,p'*DDD, and *p,p'*DDE. While *o,p'*DDE and *p,p'*DDMU are present, although not as major constituents of the fish samples, both have the same short retention times on the column used and are interfered with by a number of other unknowns as tends to be true of anything having a shorter retention time than *p,p'*DDE in these samples; therefore they were omitted because of the difficulty in identification and quantification. Kelthane was also omitted because it breaks down on this column (Morgan, 1967) to a material that has a low response and an even shorter retention time than DDMU.

For the purposes of this paper we assume that DDT is metabolized (O'Brien, 1967; Morgan, 1967; Menzie, 1969) as follows:



Since we have no measurements of Kelthane, the scope of this paper includes only the measurement of the metabolism of DDT to DDE and DDD. As mentioned earlier, the effluent from the Montrose plant was already partly metabolized (Carry and Redner, 1970). In seven samples taken between 14 August and 24 November 1970, the total DDT portion of the effluent contained 74% (range 62–84) of DDT, 5% (3–7) of DDD, and 21% (9–35) of DDE. During this period the effluent contained 2 lb or less of DDT per day. The proportions of DDT, DDD, and DDE at the time when dumping was 650 lb (295 kg) per day were 73:2:25.

At the beginning of this investigation some pesticides were separated on other columns to confirm the identification of DDT and its metabolites. Additional confirmation was obtained by dehydrochlorinating samples with alcoholic KOH which converts DDT and DDD to their respective ethylene derivatives, DDE and DDMU, but does not change the PCB, Aroclor 1254.

Because there are so many possible sources of variance to the estimates of pesticide content, we cannot obtain a precise measure of this error. Based on the least accurate measurements made in the course of analysis, the standard error of the amount of pesticide in a sample should be about plus or minus 10%. The error may be increased by shortcomings in methodology and by the presence of other peaks that interfere with those to be quantified. At low pesticide values the error increases, and it may be more like plus or minus 100% at values on the order of 10 ppb. However, the absolute error is only a few parts per billion also and makes little difference when values that differ by orders of magnitude are being compared.

In the myctophid samples, Aroclor 1254 seemed to be the only substance that contributed peaks on the chromatogram of any significance which could interfere with quantification of the DDT series. Six Aroclor 1254 peaks span the retention time range of *p,p'*DDE, *o,p'*DDD, *o,p'*DDT, *p,p'*DDD, and *p,p'*DDT (Figure 3). In all the marine samples examined, *o,p'*DDT and *o,p'*DDD are present in either very small quantities or not detectable at all unless the samples contain very large quantities of *p,p'*DDT or *p,p'*DDD. In the myctophid samples, Aroclor 1254 seems to maintain its integrity very well. There is no apparent selective breakdown of its components, and the pattern of peaks from myctophid samples containing this PCB and very little pesticide closely resemble the Aroclor 1254 standard (Figures 3 and 4).

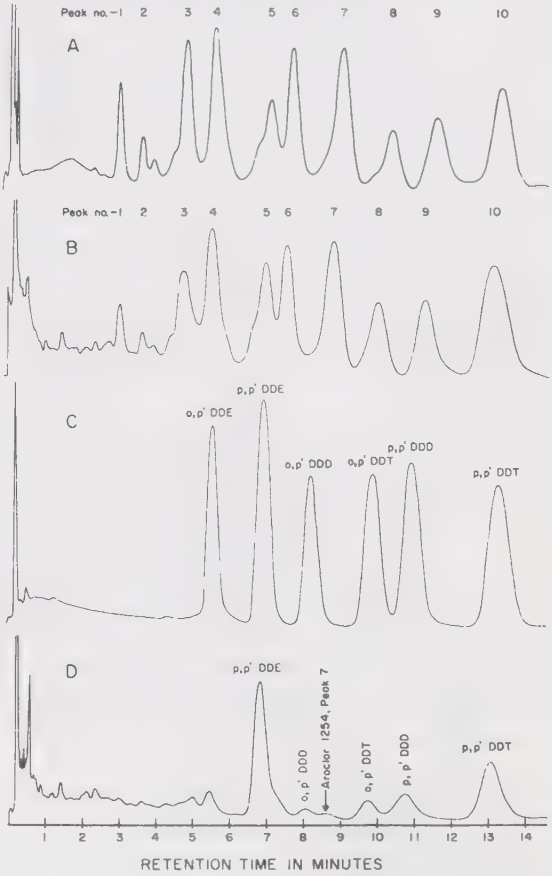


FIGURE 3.—A. Aroclor 1254 standard; column: 1.5% OV–17/1.95% QF–1, 100/120 mesh Supelcoport. B. Sample of two *Stenobrachius leucopsarus* each 20 mm standard length (SL) taken in July 1951, at CalCOFI station 70.100. About 0.54 ppm Aroclor 1254 with peak no. 5 increased slightly by 0.2 ppm DDE and peak no. 10 by 0.3 ppm DDT. Less highly chlorinated Aroclor peaks no. 1, 2, and 3 may be breaking down in the environment; more highly chlorinated peaks (no. 4 through 10) tend to maintain their integrity of pattern. Same column as A. C. Standard of six DDT analogs. Same column as A. D. Sample of a 33–mm *S. leucopsarus* taken in November 1955 at CalCOFI station 83.40. This sample contains 2.3 ppm total DDT. Because of the high DDT content of this sample, it was not concentrated as much as sample B. It probably contains at least half as much Aroclor 1254 as sample B. Same column as sample A.

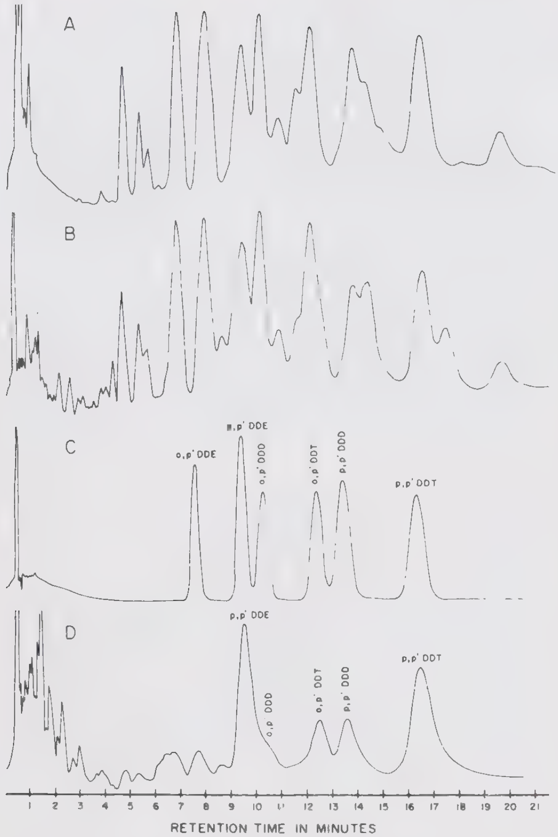


FIGURE 4.—A. Aroclor 1254 standard; column: 4% SE-30/6% QF-1, 100/120 mesh Supelcoport. B. Sample of a 28-mm *S. leucopsarus* taken in November 1955 at CalCOFI station 83.55. Aroclor 1254, 4.2 ppm; pesticides not measured. Same column as A. C. Standard of six DDT analogs. Same column as A. D. Sample of one 37-mm *S. leucopsarus* taken in March 1954 at CalCOFI station 85.45. 1.0 ppm total DDT. Same column as A.

It is apparent (Figure 3) that the seventh of the Aroclor peaks is not interfered with by the DDT series. The two ortho-para prime peaks bracketing it are generally small or absent. Therefore, it may be used to correct the DDT series for PCB interference and to quantify the Aroclor 1254.

An estimate of peak area, peak height times width at one-half peak height, was used in quantification. Increasing chart speed makes it possible to measure the width more accurately. Peak area rather than peak height is a more accurate measurement of the combined effects of two CHC when their retention times are about the same. Because GLC operating conditions may change gradually during a sample run, one pesticide standard was injected for every two samples so that each sample would have an adjacent standard for quantification.

To correct the areas of the combined peaks of the DDT series and Aroclor 1254 to the area representing pesticide only, we let X equal the area of each peak at the respective retention time of each of the DDT series and Y equal the area of Aroclor peak no. 7. Then for our operating conditions and Aroclor standard, the areas allotted to the components were:

Combined peaks	Area of Aroclor	Area of DDT series
*p,p'*DDE + Aroclor no. 5	$0.24Y$	$X - 0.24Y$
*p,p'*DDD	0	X
*o,p'*DDT + Aroclor no. 8	$0.54Y$	$X - 0.54Y$
*p,p'*DDD + Aroclor no.9	$0.73Y$	$X - 0.73Y$
*p,p'*DDT + Aroclor no. 10	$0.95Y$	$X - 0.95Y$

An estimate of Aroclor 1254 was obtained by multiplying the area of the no. 7 Aroclor peak by 12.3 and quantifying against the area of the *p,p'*DDE standard, or multiplying by 9.6 and quantifying against the area of the *p,p'*DDT standard. The subtractive corrections for the DDT series were confirmed in part for a few samples by calculating values both before and after dehydrochlorination with alcoholic KOH.

In a few samples taken far from the sewer outfall and in the earlier years, Aroclor 1254 was high enough to mask out the DDT residues except for slight increases in some peak areas (Figure 3). In such cases the pesticides were present in such small quantities that it made no appreciable difference in the overall results what small values were assigned to them. The illustrated example is an extreme case of masking.

In most of the samples the DDT residues dominated the PCB peaks and over the range of the six pesticide standards (Figure 3), only peaks no. 6 and 7 of Aroclor 1254 were evident. If DDT residues were high, peak no. 6 was evident as a widening of the base of the *p,p'*DDE peak (Figure 3).

RESULTS AND DISCUSSION

The pattern of CalCOFI stations from which the samples were obtained extends across the north flowing coastal countercurrent out into the south flowing California Current cutting across the counterclockwise eddy or eddies that develop between the two currents. At a depth of 200 m the

California Current is usually farther offshore than at the surface (Wyllie, 1966). In April and May this current moves inshore eliminating the countercurrent at the surface and sometimes at 200 m. When the California Current is offshore, the surface countercurrent develops; when it moves onshore, the surface countercurrent is absent although the southern California eddy usually persists.

The currents, and consequently the distribution of the sewer discharge, are influenced locally by such factors as the configuration of the coast, the presence of islands, the topography of the ocean floor, and the short range effects of winds and tides.

The total DDT data for the myctophids were divided into four time periods, and the average DDT value determined for all specimens taken at each station, or combined stations if they were very close together, for each time period (Figures 5-8). The total DDT content of the fish tended to be high near the sewer outlet and decreased away from the outlet. Total DDT values increased with the passage of time.

Total DDT for the purpose of this discussion consists of DDT, DDE, and DDD. Although total DDT content in the myctophids increased with time, this did not hold true for each of the three constituents. DDT increased for a few years until metabolism and dispersion equalled input and then leveled off. DDD acted in a similar manner but at a lower level. Most of the increase in total DDT after the first few years was caused by the increase in the persistent metabolite, DDE. The

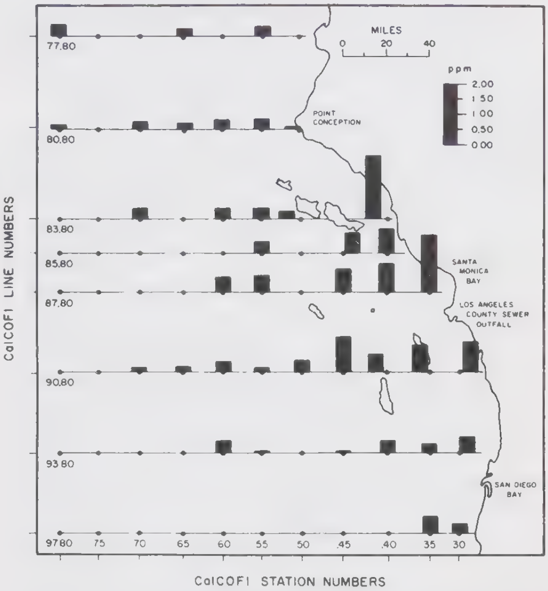
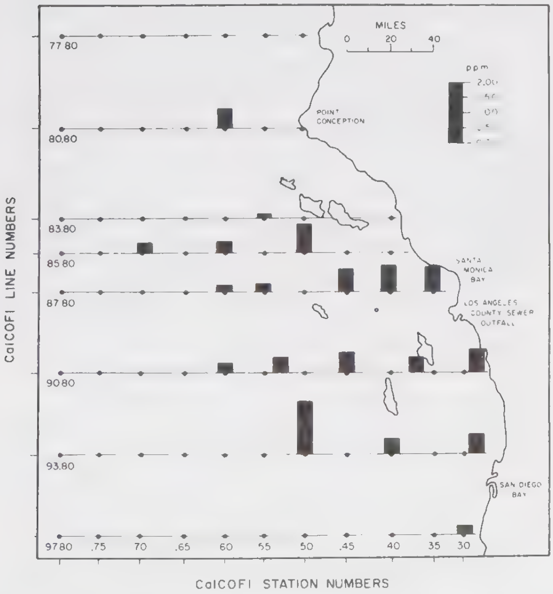

MILES
0 20 40
ppm
2.00
1.50
1.00
0.50
0.00
77.80
80.80
83.80
85.80
87.80
90.80
93.80
97.80
75 70 65 60 55 50 45 40 35 30
POINT CONCEPTION
SANTA MONICA BAY
LOS ANGELES COUNTY SEWER OUTFALL
SAN DIEGO BAY
CalCOFI LINE NUMBERS
CalCOFI STATION NUMBERS

FIGURE 6.—Average total DDT at CalCOFI stations off southern California for the 4 yr 1953–56.


MILES
0 20 40
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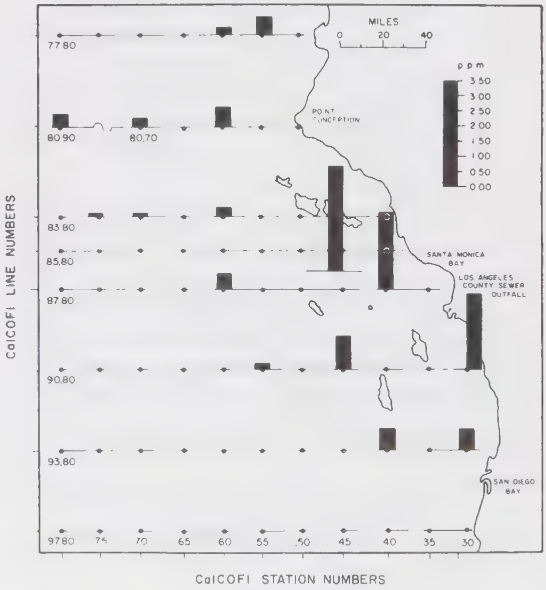
2.00
77.80
80.80
83.80
85.80
87.80
90.80
93.80
97.80
75 70 65 60 55 50 45 40 35 30
POINT CONCEPTION
SANTA MONICA BAY
LOS ANGELES COUNTY SEWER OUTFALL
SAN DIEGO BAY
CalCOFI LINE NUMBERS
CalCOFI STATION NUMBERS

FIGURE 5.—Average total DDT at CalCOFI stations off southern California for the 3 yr 1950–52.


MILES
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ppm
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3.00
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77.80
80.90
80.70
83.80
85.80
87.80
90.80
93.80
97.80
75 70 65 60 55 50 45 40 35 30
POINT CONCEPTION
SANTA MONICA BAY
LOS ANGELES COUNTY SEWER OUTFALL
SAN DIEGO BAY
CalCOFI LINE NUMBERS
CalCOFI STATION NUMBERS

FIGURE 7.—Average total DDT at CalCOFI stations off southern California for the 4 yr 1957–60.

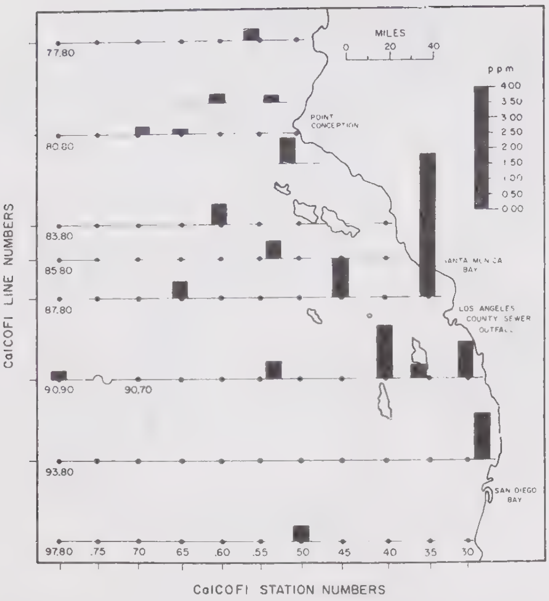

FIGURE 8.—Average total DDT at CalCOFI stations off southern California for the 6 yr 1961–66.

increase in p,p'DDE relative to p,p'DDT for the years 1950-51 through 1965-66 in the myctophids was:

Year	*Ratio of DDE to DDT*
1950–51	0.33:1.00
1952–53	0.36:1.00
1954–55	0.69:1.00
1956–57	1.06:1.00
1959–60	1.14:1.00
1961–62	2.02:1.00
1963–64	2.39:1.00
1965–66	3.96:1.00
(1970)	(4.74:1.00)
(1972)	(8.80:1.00)

These data show a 12–fold increase in the amount of DDE relative to DDT from 1950–51 to 1965–66. The ratio for the fish taken in 1970, 65–70 nautical miles southeast of the sewer outlet (in La Jolla Canyon) indicates a continuing increase in the ratios, although there were only two fish in the sample. The 1972 sample, consisting of only five myctophids, was taken west of Santa Catalina Island and about 25–30 nautical miles south southwest of the sewer outfall about 2 yr after the dumping of DDT into the sewer system had stopped. The high ratio may reflect in part continued metabolism of DDT without replenishment.

Because there are no data on the amount of DDT discharged into the ocean through the White Point sewer outfall each year, I have assumed that it was constant and discharged continuously throughout the year. Under these circumstances the amount of DDE (and DDD) entering the marine environment should gradually have increased in the earlier years until the input of DDT equalled the amount of DDT metabolized, when the input of DDE (and DDD) would also be constant. This is indicated by the initial slower increase in ratios of DDE to DDT.

If we assume that the same amount of pesticide is released into an environment each year and that it is released continuously throughout the year we may empirically represent the accumulation of the pesticide in the environment by the formula

$$Y = K(1 - S^X)$$

in which Y equals the amount of pesticide accumulated at the end of X years; K equals the maximum amount of pesticide that could be accumulated by the organism under the prevailing conditions; and S equals the "survival" rate of the pesticide for 1 yr.

In some of the years from 1949 to 1966, CalCOFI cruises were limited, and fewer samples were taken. Also the fish were not uniformly sampled with respect to distance from the sewer outfall in each of the years. But, by averaging the p,p'DDE content of all fish taken in each year and grouping years by twos, a rough indication of the increase in p,p'DDE was obtained to compare with theoretical values of the formula, $Y = K(1 - S^X)$ (Figure 9).

The almost linear increase in p,p'DDE indicates that its metabolism is very low. In fact, metabolism in this case would include p,p'DDE lost by removal from the area under study, and, therefore, the data indicate that very little was lost from this area during the years in which dumping occurred.

Because of the apparent lack of metabolism of p,p'DDE, this metabolite of p,p'DDT should give the best picture of areal and temporal buildup of a CHC in the ocean as a result of the sewer discharge.

Data on p,p'DDE content of the myctophids, year of capture (with 1949 equal to year 1), and distance in nautical miles from the sewer outlet to the place of capture were fitted to the formula:

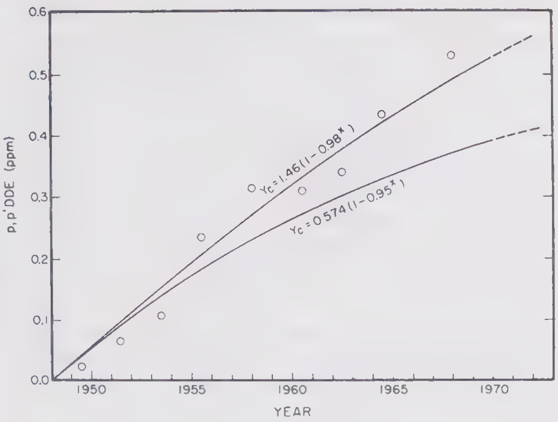

FIGURE 9.—Increase in *p,p'*DDE in the ocean off southern California, 1949–70. The points are averages of all stations combined in 2-yr groupings. Because the same patterns of stations were not run each year, myctophids were not obtained from the same stations or the same number of stations each year. Also pesticide concentrations were more dependent on distance from the point source of contamination than on year. This makes the coarse grouping of data necessary when increase in DDE with time only is considered. The two theoretical lines are computed to the formula $Y_c = K(1 - S^X)$, in which Y_c = computed value of *p,p'*DDE, K = value at which metabolism, excretion, and dispersal of DDE equals input, S = survival of DDE for 1 yr, and X = year with 1949 considered as year no. 1. The data indicate that *p,p'*DDE is very stable. For the 98% survival curve, which more closely fits the data, 90% of the equilibrium value would not be attained for 114 yr.

$$\log Y = \log a + b \log X + c \log X'$$

in which Y = calculated value of DDE in parts per billion, X = distance from sewer outfall in nautical miles, and X' = year. The data were grouped for greater ease of computation and to minimize individual variations which tend to distort the actual values transformed from log–log calculated values if not minimized by averaging.

The values determined for the above equation are:

log *a*	3.054
b (distance)	−1.062 (SE 0.057)
c (year)	1.423 (SE 0.122)

The correlation coefficients are:

multiple	0.978
partial (*b*)	−0.829
partial (*c*)	0.522

all of which are significant at P of less than 0.001.

The computed lines did not fit the data for 1949, 1950, and 1951 very well. These years were left out of the calculations because the input of DDE was rising relatively rapidly at this time and did not begin to stabilize until about 1953. Also in these earlier years, the influence of the sewer discharge of pesticide extended out to only about 100 nautical miles from the outfall. In the following years the influence of the sewer discharge increased rapidly to between 300 and 400 nautical miles from the outfall before becoming indistinguishable from the ocean background. Although there are no extensive data for any one station throughout the period under study, we can now calculate values for a theoretical station 20 nautical miles from the sewer outfall from the DDE–time–distance formula and in conjunction with the observed changes in ratios among the various DDT analogs, obtain a description of the metabolism of DDT in the marine environment as reflected in the myctophid fish, *S. leucopsarus*.

Because *o,p'*DDE was not quantified, we used only *p,p'*DDE, *p,p'*DDT, and *p,p'*DDD in the ratios. In more than 300 myctophids 30 mm or longer in standard length in which the above three constituents and *o,p'*DDT and *o,p'*DDD were measurable, *o,p'*DDT and *o,p'*DDD averaged 22.3% of *p,p'*DDT and *p,p'*DDD. In samples of commercial DDT that were tested *o,p'*DDT averaged about 25% of *p,p'*DDT.

From the calculated values of DDE and ratios of DDE to DDT, we can calculate that at our theoretical 20 mile station DDT accumulates in the fish up to 1.077 ppm when input equals metabolism. From this we may calculate that:

$$Y_t = 1.077(1 - 0.708^X)$$

in which Y_t equals calculated *p,p'*DDT and X equals the year with 1949 equal to year 1. From the values obtained (Table 1, Figure 10) we may recalculate values for DDE. These values remain essentially the same as those calculated from the DDE–time–distance formula for the later years but make allowances for lower input from DDT for the earlier years if we use the formula:

$$\begin{aligned} 2.046Y_e &= 0.368X - 1.077 + 1.077(0.708^X) \\ \text{or} \qquad Y_e &= 0.180X - 0.526 + 0.526(0.708^X) \end{aligned}$$

in which Y_e = calculated *p,p'*DDE and X equals the year and in which we assume that there is no further metabolism of DDE.

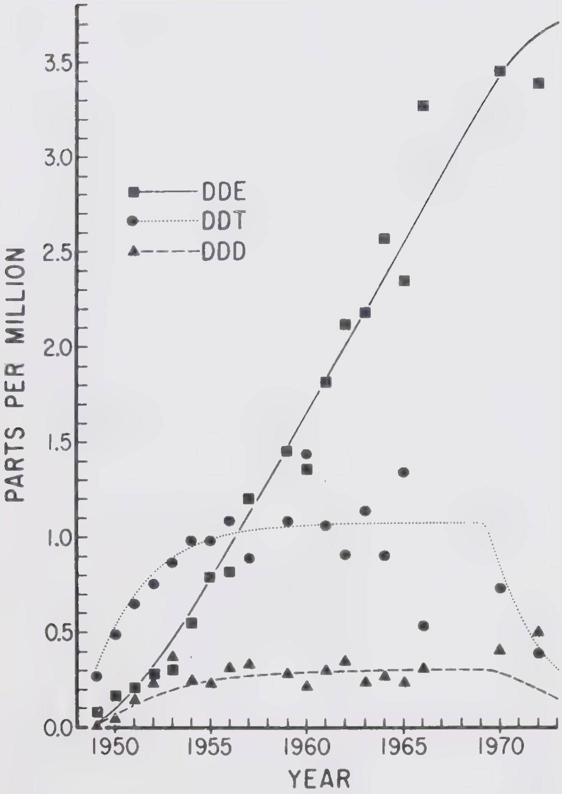

FIGURE 10.—Trends of p,p'DDE (squares), p,p'DDT (circles), and p,p'DDD (triangles) in the ocean off southern California, 1949–72, at a theoretical station 20 nautical miles from the point source of pesticide contamination. Computed lines show persistant DDE increasing until dumping of DDT wastes ceased in 1970. Both DDT and DDD increase for several years and then level off when metabolism, excretion, and dispersion equal input. Points are based on calculated total value of the three analogs distributed among them on the basis of the observed ratios of the three analogs to each other for each year. The 1972 ratios were affected by sewer cleaning operations that caused large quantities of DDD to enter the ocean.

From the calculated values of DDT and the DDD:DDT ratios we may estimate values for DDD. From these it appears that DDD accumulates in the fish up to 0.303 ppm where input equals metabolism. From this we may calculate that $Y_d = 0.303(1 - 0.525^X)$. However, this formula is based on a constant input equivalent to 0.189 ppm. The actual input from metabolism of DDT was only 0.028 ppm the first year and increased to 0.181 by the 10th year, and 0.188 by the 20th year. By adjusting for these increasing inputs we obtain accumulative values for DDD, for DDMU, and other metabolites of DDD (Table 2, Figure 10).

The percent distribution of total DDT among p,p'DDT, p,p'DDE, and p,p'DDD did not appear to change in myctophids with distance from the sewer outfall. Therefore the percent distribution which is based on large numbers of fish in most years can be used to prorate the total p,p'DDT obtained from the curves to obtain "observed" values of p,p'DDT, p,p'DDE, and p,p'DDD (Table 1, Figure 10). Both the curves and their observed values are based on observed percent changes in the composition of total DDT transformed to ppm values of the three constituents at a theoretical station 20 nautical miles from the sewer outfall.

It should be emphasized that the above description of metabolism is only an indication of what is taking place in the ocean. It neither describes the metabolism of DDT in the myctophid fish nor the metabolism in the marine environment, but rather reflects selective storage of DDT and its environmental metabolites in one species of fish.

Three factors determine the amount of CHC found in myctophid fishes: 1) The CHC present in the fish's environment during its brief life span; 2) the selective absorption of CHC through the gills and the ingestion of selected food particles; 3) and the selective storage, metabolism and excretion of CHC. Factors 2 and 3, above, should remain constant for each generation of fish. Therefore, the changes in composition of total DDT probably reflect changes occurring in the environment. However, the percent composition found in the myctophids may not represent the percent composition in the environment because of the selective nature of intake and excretion.

Some of the DDT was changed to DDE and DDD before entering the ocean. Sixteen samples of sewer discharge from the Montrose Chemical Corporation taken between 14 August 1970, and 12 May 1971, averaged 74%DDT, 20%DDE, and 6%DDD (Redner and Payne, 1971). Although these samples represented discharges averaging less than 0.5 lb (0.23 kg) a day, samples taken earlier in 1970 when dumping was estimated at 640 lb (290 kg) per day also had ratios of 73:25:2. These percent ratios are very much like the 74:23:2 distribution in the myctophids in 1949 and the 70:23:7 distribution in 1950.

Although some DDT was converted to DDD and DDE before it left Montrose, most of the metabolism took place after it was discharged from the plant. This is indicated by the percent distribution of DDT, DDE, and DDD in the myctophids in 1970, 16:75:9, by the bottom fish taken

TABLE 2.—Calculated values of *p,p'*DDT, *p,p'*DDE and *p,p'*DDD and their observed percent distribution in the myctophid fish *Stenobrachius leucopsarus*, at a distance of 20 nautical miles from the point source of pollution in the ocean off southern California for the years 1949 through 1973.

Year	Annual input (ppm)	Accumulated input (ppm)	Calculated accumulated *p,p'*DDT (ppm)	Metabolites of *p,p'*DDT		Metabolites of *p,p'*DDD (DDMU and others excreted or not measured) (ppm)	Accumulated total DDT (ppm)	Observed percent			Concentration based on observed percent		
				Accumulated *p,p'*DDE (ppm)	Accumulated *p,p'*DDD (ppm)			*p,p'*DDT (%)	*p,p'*DDE (%)	*p,p'*DDD (%)	*p,p'*DDT (ppm)	*p,p'*DDE (ppm)	*p,p'*DDD (ppm)
1949 (1)	0.37	0.37	0.31	0.03	0.02	0.01	0.36	74.4	23.3	2.3	0.27	0.08	0.01
1950 (2)	.37	.74	.54	.10	.07	.03	.70	70.0	23.3	6.7	.49	.16	.05
1951 (3)	.37	1.10	.69	.20	.12	.09	1.01	64.0	21.1	14.9	.65	.21	.15
1952 (4)	.37	1.47	.81	.33	.16	.18	1.29	58.5	21.9	19.6	.76	.28	.25
1953 (5)	.37	1.84	.88	.47	.20	.29	1.55	55.9	19.7	24.4	.87	.31	.38
1954 (6)	.37	2.21	.94	.62	.22	.42	1.79	54.8	31.1	14.1	.98	.56	.25
1955 (7)	.37	2.58	.98	.78	.24	.57	2.01	48.9	39.5	11.6	.98	.79	.23
1956 (8)	.37	2.94	1.01	.95	.26	.73	2.22	48.7	37.0	14.3	1.08	.82	.32
1957 (9)	.37	3.31	1.03	1.12	.27	.89	2.42	36.5	49.7	13.8	.88	1.20	.33
1958 (10)	.37	3.68	1.04	1.29	.28	1.07	2.61	No data					
1959 (11)	.37	4.05	1.05	1.47	.29	1.24	2.80	38.4	51.4	10.2	1.08	1.44	.29
1960 (12)	.37	4.42	1.06	1.64	.29	1.42	2.99	47.9	45.1	7.2	1.43	1.35	.22
1961 (13)	.37	4.78	1.06	1.82	.29	1.61	3.18	33.4	57.0	9.6	1.06	1.81	.31
1962 (14)	.37	5.15	1.07	2.00	.30	1.79	3.36	26.9	62.8	10.3	.90	2.11	.35
1963 (15)	.37	5.52	1.07	2.18	.30	1.97	3.55	32.0	61.3	6.7	1.13	2.17	.24
1964 (16)	.37	5.89	1.07	2.36	.30	2.16	3.73	24.0	68.7	7.3	.89	2.56	.27
1965 (17)	.37	6.26	1.07	2.54	.30	2.35	3.91	34.1	59.8	6.1	1.33	2.34	.24
1966 (18)	.37	6.62	1.08	2.72	.30	2.53	4.09	12.9	79.5	7.6	.53	3.25	.31
1967 (19)	.37	6.99	1.08	2.89	.30	2.72	4.27	No data					
1968 (20)	.37	7.36	1.08	3.07	.30	2.91	4.45	No data					
1969 (21)	.37	7.73	1.08	3.25	.30	3.10	4.63	No data					
1970 (22)	.11	7.84	.85	3.41	.29	3.28	4.56	15.9	75.3	8.8	.72	3.43	.40
1971 (23)	.00	7.84	.60	3.54	.25	3.45	4.39	No data					
1972 (24)	.00	7.84	.43	3.62	.20	3.59	4.25	9.0	79.2	11.8	.38	3.37	.50
1973 (25)	.00	7.84	.30	3.68	.15	3.70	4.14	No data					

in Santa Monica Bay in 1970, 8:87:6, and by a bottom sediment sample taken near the sewer outfall in 1971, 6:82:12. Samples of sewer water taken in 1970 that derived their DDT content from sewer sediments had ratios of 14:38:48 (Redner and Payne, 1971).

A few specimens of another myctophid, *Triphoturus mexicanus,* also showed a change in CHC ratios with time. Twenty-one specimens taken between 1950 and 1959 contained an average of 69% DDT, 9% DDD, and 22% DDE, while 12 specimens taken between 1961 and 1970 contained 23% DDT, 15% DDD, and 62% DDE. These fish were taken between Los Angeles and southern Baja California (lat 26°20′N). This species has a more southern distribution than *Stenobrachius leucopsarus,* and therefore the population was less influenced by the sewer discharge.

One might expect that DDE would be more abundant in samples taken farther from the sewer outfall, indicating older deposits, but this is not the case. The proportions are very similar in all samples, even those taken outside of the influence of the sewer. For the fish samples taken in 1969-70 for the survey, the percentages are given in Table 3.

Table 3.—Distribution of *p,p′*DDE, *p,p′*DDD, and *p,p′*DDT in fish samples by area taken, 1969–70.

Location	Number of samples	Percent as		
		DDE	DDD	DDT
Southern Baja California	8	80.6	8.9	10.5
Sebastian Vizcaino Bay	3	74.2	8.8	17.0
Cortez Bank	4	86.5	4.7	8.8
Southern California coast	6	86.0	5.1	8.9
Farnsworth Bank	6	86.9	5.6	7.5
Santa Monica Bay	8	86.6	5.8	7.6

Each sample contained several fish of the same species, and only the livers were tested. Where the pesticide levels were very high, the proportions were remarkably similar among samples. For the eight Santa Monica Bay samples, the DDE ranged from 85.2 to 87.7%, DDD from 5.1 to 6.6%, and DDT from 5.7 to 9.1%.

The high proportions of DDE relative to DDT and DDD seem to be typical of fishes, porpoises, and crustaceans in the ocean off southern California (Tables 4 and 5). In six adult pelicans taken on Anacapa Island in 1969 (Keith et al., 1970), DDE made up 99% of the total DDT found in the fat, and 93% in eggs taken at the same time. Lamont, Bagley, and Reichel (1970) tested 10 pelican eggs from the same place and year and found that DDE constituted 96% of the total.

Stout (1968) gives data for 17 samples representing seven species of marine fishes taken off Washington and Oregon. In these, DDE averaged

Table 4.—Percent distribution of total DDT and ratio of DDD to DDT in rockfishes and sablefish from Santa Monica Bay. Major dumping of DDT wastes into sewer system stopped in April 1970. Samples of May 1970 and August 1971 are averages of five separate samples each for fat, liver, and flesh. In each of these 15 samples the ratio of DDE to DDT was greater than one.

Species	Part tested	Total DDT (ppm)	Percent distribution			Ratio
			DDE	DDD	DDT	DDD:DDT
May 1970:						
Sebastes paucispinis	Liver	519.0	86.3	5.6	8.1	0.69:1.00
S. paucispinis	Flesh	11.6	80.6	8.8	10.6	.82
S. miniatus	Liver	162.0	87.0	5.6	7.4	.75
S. miniatus	Flesh	16.0	92.3	trace	7.7	.0?
S. constellatus	Liver	1,026.0	87.7	5.5	6.8	.80
S. constellatus	Flesh	57.2	88.2	5.5	6.3	.86
S. constellatus	Fat	2,588.0	85.0	7.0	8.0	.87
Anoplopoma fimbria	Liver	103.0	87.3	5.8	6.9	.85
A. fimbria	Flesh	23.4	81.2	10.1	8.7	1.15
August 1971:						
S. paucispinis and S. mystinus	Liver	156.0	84.0	10.3	5.7	1.78
A. fimbria	Liver	38.0	84.2	12.9	3.9	4.45
January 1972:						
S. paucispinis	Liver	17.0	78.5	15.5	6.0	2.58
S. paucispinis	Flesh	.20	81.4	12.7	5.9	2.15
S. paucispinis	Fat	115.0	78.8	16.1	5.1	3.15
August 1971:						
Bottom sample	Mud		82.0	72.0	6.0	2.00

Table 5.—Distribution of *p,p'*DDE, *p,p'*DDD and *p,p'*DDT in various animals from southern California marine waters. Porpoises found dead on beach north of San Diego, various dates May 1970. Fishes and crustaceans taken in net haul in San Pedro Channel 4 August 1971.

Species	Organ tested	Standard length (mm)	Wet weight (g)	Total DDT (ppm)	Percent as		
					DDE	DDD	DDT
Porpoises:							
Lagenorhynchus obliquidens	flesh			84.	92.0	2.3	5.7
Delphinus sp.	flesh			208.	86.5	5.8	7.7
Delphinus sp	flesh			31.	85.0	7.2	7.8
Delphinus sp.	liver			44.	90.7	4.8	4.5
Delphinus sp.	liver			300.	92.0	4.0	4.0
Delphinus sp.	head oil			196.	89.8	2.6	7.6
Delphinus sp.	blubber			497.	88.5	3.4	8.1
Fishes:							
Leuroglossus stilbius	whole	84	5.20	.49	75.9	11.6	12.4
Melanostigma pammelas, eelpout	whole	89	2.40	5.63	87.9	2.7	9.4
Argyropelecus sp., hatchetfish	whole	30	.50	.09	49.5	7.6	42.9
Cyclothone acclinidens	whole	48	.36	2.01	80.7	4.7	14.6
Cyclothone acclinidens	whole	43	.37	.64	76.1	6.9	17.0
Cyclothone acclinidens	whole	47	.39	2.46	83.2	5.9	10.9
Cyclothone acclinidens	whole	38	.18	3.56	89.5	4.5	6.0
Cyclothone acclinidens	whole	34	.15	1.55	84.9	8.5	6.6
Crustaceans:							
Gnathophausia gigas, pelagic mysid	whole		.42	.55	76.7	7.2	16.1
Sergestes sp.	whole		.64	4.38	85.1	6.1	8.8
Sergestes sp.	whole		.38	4.59	82.9	6.1	11.0
Nematoscelis sp., euphausiid	whole		.019	.35	90.3	4.3	5.4
Nematoscelis sp., euphausiid	whole		.043	.26	90.2	3.0	4.9

52% (26–81), DDD 20%, and DDT 28% of total DDT.

Keith and Hunt (1966) list DDT content for samples of mammals, birds, and freshwater fishes taken throughout California. The proportion of DDE tends to be high in categories that include birds of prey and fish eating birds, but varies considerably in their other samples. In their warm-water fish samples and the fish eating birds, white pelican, western grebe, and common egret, DDD is unusually high. This may be because of the former use of DDD as a spray on some California lakes (Murphy and Chandler, 1948; Brydon, 1955; Hunt and Bischoff, 1960).

Following the cessation of DDT dumping into the ocean off Los Angeles in 1970, a change occurred in the DDD:DDT ratios found in fish samples. The five *S. leucopsarus* taken in April 1972 contained 79% DDE, 12% DDD, and 9% DDT. Each of the five specimens contained more DDD than DDT. In the period 1949–70, only 8 out of more than 500 *S. leucopsarus* tested contained more DDD than DDT. The five myctophids taken in April 1972 ranged from 40 to 50 mm SL, indicating that most or all of their growth had taken place since dumping stopped in 1970.

The shift in DDD:DDT ratios also appeared in some other species. The ratios in rockfishes and sablefish, *Anoplopoma fimbria*, taken in Santa Monica Bay in May 1970, indicated that DDT was more abundant than DDD while 15 and 20 mo later the reverse was true (Table 4, Figure 11). The pelagic crustaceans and fish taken in the midwater trawl in August 1971 (Table 5) did not show the increased DDD to DDT ratio as did the bottom fish taken at that time, or the five *S. leucopsarus* taken in April 1972. A mud sample taken in August 1971 (Table 4, Figure 12) about 3 nautical miles from the White Point sewer outfall contained about twice as much DDD as DDT.

The work of Burnett (1971) on DDT residues in the sand crab along coastal California showed that the high ratios of DDD to DDT were a local condition. Twelve samples taken in November 1970 and February 1971 from eight stations on either side of the White Point sewer outfall between 33°22′N and 34°28′N contained more DDD than DDT in all but two samples. The 11 stations north and south of this area all contained less DDD than DDT. The four samples taken closest to the outfall averaged more than three times as much DDD as DDT.

This shift in DDD:DDT ratios was undoubtedly caused by the deposits in the sewer system. CSDLAC cleaning operations started in December 1970, and ended in July 1971. Although large quantities of these deposits were removed directly from the sewers, additional large quantities were moved through the system to the White

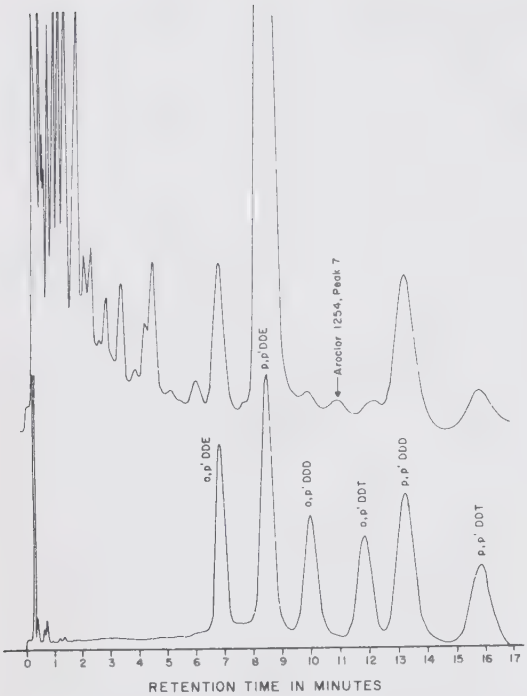

FIGURE 11.—Chromatogram of DDT analog standard and of a fat sample from *Sebastes paucispinis* taken in Santa Monica Bay 7 January 1972. *p,p'*DDE (98 ppm) is off scale. Following cessation of dumping of DDT wastes and flushing out of sewer lines in 1970, *p,p'*DDD (15 ppm) has exceeded *p,p'*DDT (6.1 ppm) in most fish specimens tested. Prior to cessation of dumping and flushing of sewer lines, DDT was almost always present in greater quantities than DDD.

Point plant and out into the ocean. Sewer water from these deposits contained 48% DDD as opposed to 2–6% in the original Montrose discharges, and although the total amount of DDT and its metabolites was much less than before April 1970, the total amount of DDD entering the ocean appeared to be several times greater than it had been before the dumping stopped in April. This would account for the increase in DDD in the myctophids taken in 1972 rather than the expected decrease indicated by the calculated line (Figure 10, Table 1). A mud sample taken from the ocean floor a few miles from the sewer outfall in July 1971, just after the sewer cleaning operations ceased contained 6% DDT, 82% DDE, and 12% DDD (Figure 12). This compares favorably with the myctophids taken in April 1972, 9:79:12, and the *S. paucispinis* fat samples (Figure 11) taken in January 1972, 5:79:16, and indicates that the fish reflect the values of these analogs in the environment fairly well.

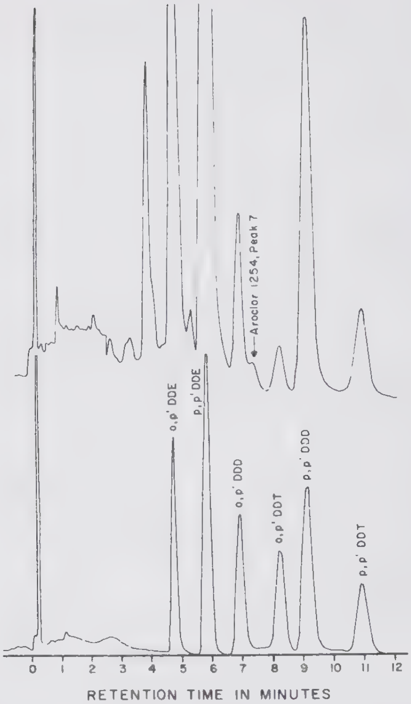

FIGURE 12.—Chromatogram of DDT analog standard and sample of mud from the ocean floor in the Los Angeles area taken in August 1971, 16 mo after most dumping of DDT wastes stopped. DDD greatly exceeds DDT. This may have resulted from the sewer cleaning operations, or it may have been the condition existing before and merely reflect what the biota can excrete more easily. In the *Sebastes* chromatogram (Figure 11), the *o,p'*DDE peak is within the limits of the right proportions to *p,p'*DDE for it to be considered *o,p'*DDE. In the mud sample it is much too high and may be DDMU (a metabolite of DDD) which has the same retention time on this column as *o,p'*DDE.

The most noticeable difference between the pesticide metabolites in the fish (Figure 11) and the mud (Figure 12) were the two prominent peaks preceding *p,p'*DDE. The peak at the locus of *o,p'*DDE also may contain DDMU, a metabolite of DDD. The other peak could be a metabolite of Kelthane. However, several dozen additional mud samples tested subsequently did not contain these peaks except for expected amounts of *o,p'*DDE. The mud sample (Figure 12) was run while we were experimenting with methods of determining pesticide content of the mud samples. The subsequent samples were run after we had settled on a different method that gave maximum recovery of DDT, DDD, and DDE without special regard to other CHC. These subsequent mud samples yielded chromatograms almost identical with those of fish and other biological samples from the same general area.

There was also a large decrease between May 1970 and January 1972, in total pesticides in the fish taken in Santa Monica Bay (Table 4). The *S. paucispinis* taken in 1972 were smaller than those taken in 1970 which may account in part for the lower values. The five specimens taken in January 1972, averaged 312 mm total length. Phillips (1964) gives the total length of this species at age 2 as 267 mm and at age 3 as 343 mm. Thus, most of the growth of these specimens had taken place since dumping stopped.

On land where soil has been subjected to DDT spraying for long periods of time, the situation is very different. In New York State vineyard soils (Kuhr, Davis and Taschenberg, 1972) the residues consisted of 73% DDT and 27% DDE after 24 yr of spraying with DDT. In Oregon (Kiigemagi and Terriere, 1972) samples of soil from one orchard contained 80% DDT, 17% DDE, and 3% DDD after 25 yr of spraying, while soil samples from another orchard in a different area contained 78% DDT, 14% DDE, and 8% DDD after 24 yr. Forests in New Brunswick, Canada (Yule, 1973) were sprayed heavily from 1956 to 1967 in which year spraying with DDT ceased. Many samples taken of soils in this area in 1968 contained 92% DDT and 8% DDE. Three years later a second sampling of the soils in the same locality contained 90% DDT and 10% DDE. DDD was present only in trace amounts in both sampling years.

As a general rule soil samples from land areas that have been sprayed with DDT tend to contain a much higher proportion of DDT than DDE or DDD even after many years. This is not necessarily true of the fauna that inhabit the land unless their contamination is the result of recent spraying. Keith and Hunt (1966) give examples of a number of species of mammals and birds in which the proportions of the three analogs vary greatly.

Within some species of birds, which are more wide ranging than mammals, there seems to be remarkable uniformity in the proportions of the three analogs. Martin and Nickerson (1972) tested 125 10-bird samples of starlings from throughout the (48) United States. These samples averaged 91% DDE, 3% DDD, and 6% DDT. Although the total residues ranged from 0.05 to 15 ppm, in only two samples did the amount of DDD exceed DDT, and in only one did the amount of DDT exceed DDE.

The proportions of the three analogs of DDT in the starlings is very similar to the proportions found in the fish taken in Santa Monica Bay in 1970 (Table 4), in the porpoises found dead on the beach in 1970, and the small fishes and invertebrates taken off Los Angeles in the mid–water trawl in 1971 (Table 5). And, in fact, except in cases of recent contamination by DDT, most fauna have tended to approach these proportions in recent years. This is in spite of the fact that soil samples from areas of land that have long histories of spraying with DDT almost without exception contain very high proportions of DDT. From this it would appear that the selective storage, metabolism, and excretion of DDT is somewhat similar for all animals.

When investigators first became aware of the pesticide problem, methods of measuring residues were considerably less refined than they are at present, and few samples were run. Very little work has been done on preserved specimens from these earlier years. But, in view of the similarity in proportions of DDE and DDT in so many different species in recent years, it seems probable that the increase in DDE and the change in ratios of DDE and DDT in *S. leucopsarus* are descriptive of the general change in these analogs that has taken place in the earth's environment.

There was no pattern discernible in the distribution of Aroclor 1254. In 472 myctophid samples taken between 1949 and 1966, the median values of Aroclor 1254 fluctuated around 0.17 ppm and showed no trend with time. Sixty–eight percent of the samples contained less than 0.25 ppm. The only indication of an areal relationship was that while the three stations closest to the White Point sewer outfall, and the city of Los Angeles (CalCOFI stations 87.35, 90.28, and 90.30) constituted only 8% of the total samples, they accounted for 34% (12 out of 35) of the myctophids containing more than 1ppm of Aroclor 1254. However, there were some samples taken 175–200 nautical miles offshore that contained more than 1 ppm, and there were others taken near shore in the Los Angeles area that contained none or traces only. These higher values could result from the myctophids ingesting nondigestible particles of man-made substances either while feeding or accidentally while in the cod end of the plankton net.

In the larger fish taken in the Los Angeles area, the high values of the DDT residues tend to mask the presence of Aroclor 1254. What might be recorded as a trace amount could actually be a rather significant amount in view of the dilute solutions of sample used in such cases in order to keep the DDT residue recordings on scale.

SUMMARY

1. Between 1949 and 1970, total DDT increased in the ocean off southern California. The major source of this insecticide apparently was wastes discharged into the Los Angeles County sewer system by a major manufacturer of DDT.

2. As measured in the myctophid fish, *Stenobrachius leucopsarus*, *p,p'*DDT and *p,p'*DDD increased for several years until metabolism, excretion, and dispersion equalled input, at which point the content of these CHC stabilized in the fish.

3. The more persistent, less easily metabolized *p,p'*DDE continued to increase in *S. leucopsarus* throughout the time period under study. The amount of *p,p'*DDE decreased with distance from the sewer outfall.

4. During the earlier years the abundance of the other analogs in decreasing order was *p,p'*DDT, *p,p'*DDE, and *p,p'*DDD. During the later period through 1970, the more persistent *p,p'*DDE became more abundant than *p,p'*DDT. Following cessation of dumping, in 1970, *p,p'*DDD became more abundant than *p,p'*DDT in the myctophids and most of the other fish species tested.

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I am especially indebted to E. H. Ahlstrom for sacrificing part of his collection of the myctophid fish, *S. leucopsarus,* for the present study. Shirley Imsand donated the five myctophids taken in 1972 on the University of Southern California MV *Velero IV*. Carol Talkington assisted in some of the analyses. I am indebted also to R. Lasker for his invaluable criticism and guidance in the preparation of the paper and to V. McClure and W. Rommel for technical advice and assistance. This work was supported in part by NOAA, Office of Sea Grant, under grant #UCSD 2-35208 with the Institute of Marine Resources, University of California.

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7423

ANALYSIS OF MIGRATIONS AND MORTALITY OF BLUEFIN TUNA, *THUNNUS THYNNUS*, TAGGED IN THE NORTHWESTERN ATLANTIC OCEAN[1,2]

F. J. Mather III,[3] B. J. Rothschild,[4] G. J. Paulik,[5] and W. H. Lenarz[4]

ABSTRACT

An analysis is presented on the release and return data from bluefin tuna, *Thunnus thynnus*, tagged in the northwest Atlantic Ocean from 1954 to 1970. There was an apparent northward movement of fish from the New Jersey area as the fishing seasons progressed. Tag returns from bluefin released in the Long Island and southern New England areas tended to be to the north at first and then to the south. Mean distances between release and return tended to be greater for fish released in the New Jersey area than for the other two areas. Estimates of mortality rates for tagged bluefin were made using the Chapman-Robson method and then adjusted for Type-I and Type-II tag shedding and Type-I tagging mortality. The average estimate of instantaneous fishing mortality is 0.57 and other losses (natural, tagging, and emigration) is 0.68 on an annual basis. The estimate of other losses is considerably higher than the natural mortality that would be expected for bluefin. Evidence is presented suggesting that the rate of emigration may be quite high. The average single season exploitation rate of tagged bluefin was estimated to be 0.33. It was noted that since bluefin may be both immigrating to and emigrating from the fishery the estimate of exploitation may not be representative of the entire population. Even though validity of available effort data is questionable, regression estimates of mortality and survival rates were made using catch per effort data. These estimates of survival are lower than those obtained using the Chapman-Robson method.

The data which form the basis for this report were assembled by the first author. This study is based upon releases of tagged bluefin tuna, *Thunnus thynnus*, that were made by a variety of organizations and individuals under the coordination of the Woods Hole Oceanographic Institution Cooperative Game Fish Tagging Program at various locations along the middle Atlantic bight of North America from July 1954 to August 1970 and returns of these tags to the end of 1970. Additional returns are expected in the future from more recent releases.

MIGRATIONS

Because of the variety of methods, locations, and dates of release, we needed to assemble the data by relatively homogeneous release groups. The criterion for constructing a release group for analysis of migrations was to develop homogeneous time-location strata of releases from which a minimum of 20 tags were recovered. This procedure allowed us to work with homogeneous groups, but eliminated roughly 10% of the recovered tags from our analysis. Table 1 summarizes these release groups and Figure 1 shows their localities. We can see from Table 1 that during the study period the tagging operations tended to shift from the New Jersey coast, to the New York coast, to the southern New England coast, and that releases in July tended to be south of those made in August or September.

Tagging data have been used to show some of the longer migrations of the bluefin tuna (Food and Agriculture Organization, 1972). We examined the shorter term recoveries from an analytic point of view. In order to do this, we made use of a method developed by Rothschild (Bayliff and Rothschild, in press). Using this method each release group was stratified into intervals of time at liberty. Release vectors (latitude and longitude) for each release group were used to compute an average or common release vector. Each recapture vector for the group was then standardized to the common release vector. The standardized vectors were then used to find 1) the average recapture vector and 2) the determinant of the recapture

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[1] This paper is dedicated to the memory of Gerald J. Paulik. He was a good friend and colleague and made important contributions to the theory of tagging.

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TABLE 1.—Release groups used for analysis of migrations of tagged bluefin tuna.

	General location of release					
	New Jersey Coast		Long Island Coast		Southern New England	
Release date	Group No.	No. of returns	Group No.	No. of returns	Group No.	No. of returns
July 1964	2A	33				
	2B	32				
	2C	27				
Aug. 1964			3	33		
July 1965	4A	36				
	4B	86				
	4C	38				
Aug. 1965	5A	22	5B	47	5C	24
July 1966	6A	114				
	6B	127				
	6C	45				
	6D	85	6E	62		
Aug. 1966			7A	20	7C	85
			7B	81	7D	36
					7E	55
					7F	203
					7G	177
Sept.-Oct. 1966			8	23		
July 1967	9A	23				
	9B	94				
Sept. 1967			10	27		
July 1968	11A	21	11B	39		
July 1969			12	24		
Aug. 1969					13	40
Sept. 1969					14	22
July 1970					15	17
Aug. 1970					16	25
1954-63					17	24

variance-covariance matrix. The determinant of the recapture variance-covariance matrix is proposed by Bayliff and Rothschild as an index of the dispersal of the fish. When the distance of the recoveries from one another is large, the determinant is large.

It should be noted that the vectors computed by this method are not on a per-unit-effort basis so that "migration patterns" reflect not only the apparent movement of the fish, but also the distribution of fishing effort. In order to more fully understand the nature of short-term movements, it will be necessary to study in some detail the complex problem of the distribution of bluefin tuna in the northwest Atlantic. Preliminary to more detailed analysis of these statistics, we surveyed some of the main features of the data, of which some are tabulated in Table 2.

First we considered the direction of movement. Figure 2 contains a synthesis of these data and shows the direction of movement by tagging location and time at liberty. It is implicit that we treated each symbol as reflecting the behavior of a sample of fish from the same statistical population. The main features of Figure 2 are that fish tagged off New Jersey in July tended to move in an eastward direction and both north and south during the first 2 wk at liberty, but then movement became strongly directed to the northeast. Fish released in the Long Island area initially tended to move toward the north, but after the first 30 days, their movement appeared to have been concentrated to the west and south. The same conclusion may be obtained from the southern New England releases.

An examination of the mean distance (Figure 2) shows fish released off New Jersey tended to be recovered at a slightly greater distance to the north than the south. The fish moved approximately 7 or 8 miles per day. By the second 15-day period, the fish moved about 60-100 miles to the northeast. The pattern for Long Island releases, based on only a few observations, shows that movement distance of these fish during 1-15 days was approximately the same as that for the New Jersey releases. The short-term recoveries of southern New England tagged fish reflect even less average distances than New Jersey short-term releases suggesting that either the fish off southern New England moved less than off New

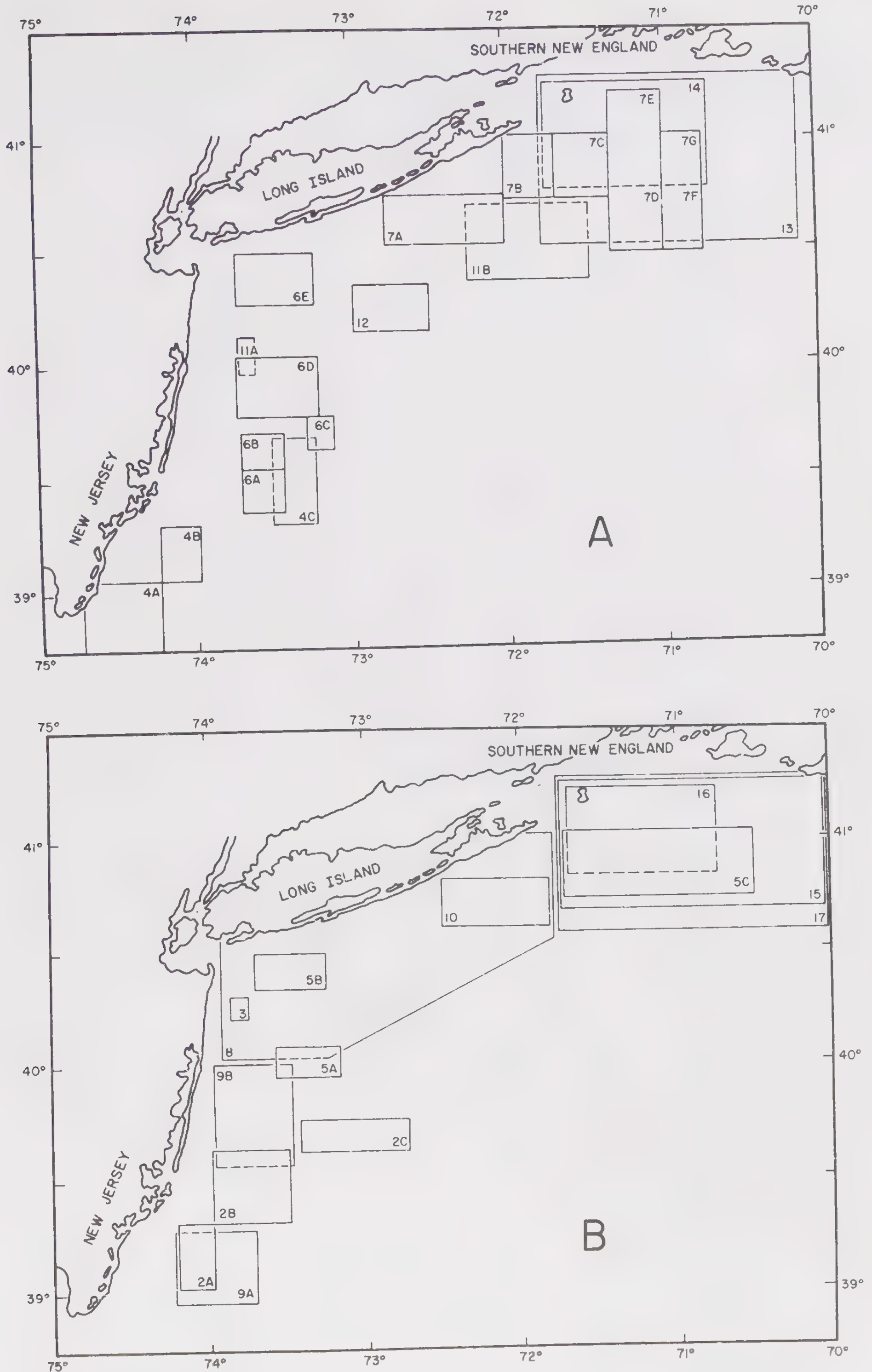
75°
74°
73°
72°
71°
70°
41°
40°
39°
SOUTHERN NEW ENGLAND
LONG ISLAND
NEW JERSEY
14
7E
7C
7G
7B
7D
7F
7A
13
11B
6E
12
11A
6D
6C
6B
6A
4C
4B
4A
A
16
5C
15
10
17
5B
3
8
5A
9B
2C
2B
2A
9A
B

FIGURE 1.—Part A and Part B: Map of middle Atlantic bight showing release group locations of tagged bluefin tuna.

TABLE 2.—Summary of statistics on movements of tagged bluefin tuna. All distance measures are nautical miles.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10^4)	Mean distance	No. of fish	Release month	General release location
2A	1-15	26.5	34.1	2.3	50.5	13	July 1964	N.J.[3]
	16-30	74.2	74.9	26.0	114.0	9		
	31-60					1		
	61-180					0		
2B	1-15	−9.2	11.4	2.9	31.8	18	July 1964	N.J.
	16-30	25.1	58.5	1.4	89.7	7		
	31-60					2		
	61-180					0		
2C	1-15	−7.2	−15.0	1.3	29.6	14	July 1964	N.J.
	16-30					1		
	31-60					1		
	61-180					0		
3	1-15	8.0	12.2	0.3	32.6	12	Aug. 1965	L.I.[4]
	16-30					1		
	31-60					0		
	61-180					0		
4A	1-15	12.0	18.3	3.8	33.6	18	July 1965	N.J.
	16-30	83.6	52.8	11.7	102.0	8		
	31-60					1		
	61-180					1		
4B	1-15	20.9	7.4	8.7	46.4	39		N.J.
	16-30	70.8	21.2	0.2	74.6	28		
	31-60					3		
	61-180					0		
4C	1-15	25.3	−16.6	13.4	47.9	17	July 1965	N.J.
	16-30	62.3	3.1	1.1	64.8	13		
	31-60					0		
	61-180					0		
5A	1-15	25.8	−15.4	19.4	48.5	9	Aug. 1965	N.J.
	16-30	53.5	5.4	17.2	60.4	12		
	31-60					0		
	61-180					0		
5B	1-15	24.8	−17.9	9.5	47.2	8	Aug. 1965	L.I.
	16-30	44.8	−1.8	36.0	54.9	5		
	31-60					0		
	61-180					0		
5C	1-15					0	Aug. 1965	S.N.E.[5]
	16-30					0		
	31-60					0		
	61-180					0		
6A	1-15					2	July 1966	N.J.
	16-30					3		
	31-60	59.1	25.9	18.7	86.4	11		
	61-180	57.0	−11.1	0.01	58.6	23		
6B	1-15					4	July 1966	N.J.
	16-30	52.8	39.6	0.2	76.7	5		
	31-60	62.2	70.0	90.9	112.0	20		
	61-180					4		
6C	1-15					0	July 1966	N.J.
	16-30					2		
	31-60					1		
	61-180	39.9	−23.7	0.002	46.7	9		
6D	1-15	−5.5	5.6	62.3	41.1	10	July 1966	N.J
	16-30	4.0	3.3	1.7	20.7	6		
	31-60	30.6	15.6	51.9	64.7	9		
	61-180	30.0	−13.2	0.006	33.1	14		

See footnotes at end of table.

TABLE 2.—Continued.

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x10^4)	Mean distance	No. of fish	Release month	General release location
6E	1-15	−28.2	3.0	1.8	35.9	14	July 1966	L.I.
	16-30	5.0	58.1	36.0	82.4	6		
	31-60					3		
	61-180	−3.8	−3.6	1.2	16.8	10		
7A	1-15					1	Aug. 1966	L.I.
	16-30					2		
	31-60					1		
	61-180					0		
7B	1-15	0.6	22.1	0.8	26.8	11	Aug. 1966	L.I.
	16-30	−11.4	−15.5	8.8	52.4	7		
	31-60					1		
	61-180					0		
7C	1-15	−2.0	6.0	1.3	17.9	9	Aug. 1966	S.N.E.
	16-30	−3.6	6.0	1.0	28.9	8		
	31-60					1		
	61-180					0		
7D	1-15	13.2	2.5	6.2	28.2	10	Aug. 1966	S.N.E.
	16-30	7.2	−14.9	12.0	46.5	8		
	31-60					1		
	61-180					0		
7E	1-15	−17.3	2.6	8.8	29.3	15	Aug. 1966	S.N.E.
	16-30	−8.8	−21.7	30.3	50.3	5		
	31-60					1		
	61-180					0		
7F	1-15	7.5	−20.0	4.5	36.0	39	Aug. 1966	S.N.E.
	16-30	7.5	−17.4	3.3	28.9	65		
	31-60	1.3	−26.2	15.6	48.0	14		
	61-180					1		
7G	1-15	−3.8	−19.1	3.0	32.2	37	Aug. 1966	S.N.E.
	16-30	−0.7	−15.9	3.1	29.9	50		
	31-60	−4.6	−24.6	12.8	48.0	14		
	61-180					1		
8	1-15					1	Sept.- Oct. 1966	L.I.
	16-30					0		
	31-60					0		
	61-180					0		
9A	1-15					2	July 1967	N.J.
	16-30	87.7	12.7	0.003	69.1	9		
	31-60	86.8	26.8	9.4	76.6	8		
	61-180					0		
9B	1-15	−18.4	−7.1	1.0	27.4	14	July 1967	N.J.
	16-30	13.1	−3.6	1.7	24.0	12		
	31-60	27.0	7.1	13.5	39.3	47		
	61-180					2		
10	1-15					0	Sept. 1967	L.I.
	16-30					0		
	31-60					2		
	61-180					0		
11A	1-15					0	July 1968	N.J.
	16-30					2		
	31-60					0		
	61-180		−4.0	0.008	22.8	9		
11B	1-15	5.8	22.4	4.2	32.8	13	July 1968	L.I.
	16-30	10.4	35.8	0.3	39.9	11		
	31-60					1		
	61-180					4		
12	1-15					4	July 1969	L.I.
	16-30					0		
	31-60					4		
	61-180					0		

See footnotes at end of table.

TABLE 2.—Continued

Release group	Time at liberty (days)	Mean miles N-S[1]	Mean miles E-W[2]	Determinant (x 10⁴)	Mean distance	No. of fish	Release month	General release location
13	1-15					1	Aug. 1969	S.N.E.
	16-30					1		
	31-60					1		
	61-180					0		
14	1-15					0	Sept. 1969	S.N.E.
	16-30					0		
	31-60					0		
	61-180					0		
15	1-15					3	July 1970	S.N.E.
	16-30	−1.7	−20.6	3.5	28.1	9		
	31-60	−24.4	−6.8	0.5	28.2	5		
	61-180					0		
16	1-15	−13.1	−14.7	2.0	28.3	9	Aug. 1970	S.N.E.
	16-30	−33.0	−11.6	69.6	67.7	7		
	31-60					3		
	61-180					1		
17	1-15					0	1954-63	S.N.E.
	16-30					3		
	31-60	−.2	−10.4	222.9	57.1	5		
	61-180					0		

[1] Positive values signify northward movement. Negative values signify southward movement.
[2] Positive values signify eastward movement. Negative values signify westward movement.
[3] New Jersey.
[4] Long Island.
[5] Southern New England.

Jersey or that the intensity of the southern New England fishery was greater than that off New Jersey. While the latter may be true, there may be alternative interpretations and additional analysis is required. It is also suggested that analysis be undertaken for tags returned after the season of release.

MORTALITY ESTIMATION

The number of recoveries per year from releases by year, months within years, and various groupings of years, months, and release locations were employed to estimate the survival rates for young bluefin in the middle Atlantic bight of North America. The first analyses were run using only the data employed to form the basic groups as defined in the migration analysis, thus eliminating some releases which were substantially different with respect to their location and/or time of release than for most of the fish tagged. Although this reduced the numbers of returns used, it probably did not greatly affect the estimates of mortality rates.

Method of Release

In all years since 1961, with the exception of 1963, tuna were captured for tagging by both sport and commercial gear (purse seine). In Table 3 the proportions of tagged fish returned were compared for the two methods of original capture. Five of the nine chi-square tests of the hypotheses of homogeneity indicate highly significant differences in the return percentages between the types of gear used to capture the tuna for tagging. When only the 5 yr with significantly different return rates for the types of gear, i.e., 1965, 1966, 1968, 1969, and 1970 are considered, higher return percentages were obtained for sport tagged fish in 4 of

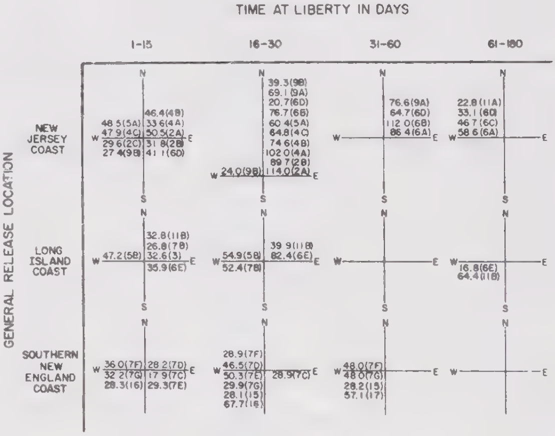
TIME AT LIBERTY IN DAYS
1-15
16-30
31-60
61-180
GENERAL RELEASE LOCATION
NEW JERSEY COAST
LONG ISLAND COAST
SOUTHERN NEW ENGLAND COAST
N
S
E
W
48.5(5A)
47.9(4C)
29.6(2C)
27.4(9B)
46.4(4B)
33.6(4A)
50.5(2A)
31.8(2B)
41.1(6D)
39.3(9B)
69.1(9A)
20.7(6D)
76.7(6B)
60.4(5A)
64.8(4C)
74.6(4B)
102.0(4A)
89.7(2B)
24.0(9B)
114.0(2A)
76.6(9A)
64.7(6D)
112.0(6B)
86.4(6A)
22.8(11A)
33.1(6D)
46.7(6C)
58.6(6A)
47.2(5B)
32.8(11B)
26.8(7B)
32.6(3)
35.9(6E)
54.9(5B)
52.4(7B)
39.9(11B)
82.4(6E)
16.8(6E)
64.4(11B)
36.0(7F)
32.2(7G)
28.3(16)
28.2(7D)
17.9(7C)
29.3(7E)
28.9(7F)
46.5(7D)
50.3(7E)
29.9(7G)
28.1(15)
67.7(16)
28.9(7C)
48.0(7F)
48.0(7G)
28.2(15)
57.1(17)

FIGURE 2.—Summary of mean distance and direction of migration of tagged bluefin tuna stratified by time at liberty and by general area of release. Distances are in nautical miles. Release group numbers are given in parentheses.

TABLE 3.—Chi-square tests of equality of return probabilities between sport and commercial gear releases of tagged bluefin tuna in the northwestern Atlantic Ocean. Each test has 1 degree of freedom.

	Sport			Commercial			
Year	Release	Return	Return rate (%)	Release	Return	Return rate (%)	Chi-square value
1961	129	7	5.4	21	0	0	1.20
1962	52	4	7.7	25	0	0	2.03
1964	10	3	30.0	455	128	28.1	0.02
1965	43	17	39.5	1,629	244	15.0	19.18**
1966	187	84	44.9	3,772	1,094	29.0	21.60**
1967	14	3	21.4	614	183	29.8	0.46
1968	41	11	26.8	219	104	47.5	5.98*
1969	244	91	37.3	92	15	16.3	13.63**
1970	425	162	38.1	32	6	18.8	4.80*

**Significant at the 0.01 level.
*Significant at the 0.05 level.

the 5 yr. The data cannot be pooled over years to increase the numbers in individual cells in the chi-square tables since the recovery percentages and numbers tagged vary so greatly from year-to-year.

However, the Mantel-Haenszel test can be used to examine the data in toto (Snedecor and Cochran, 1967:255-256). The calculations resulted in a value of 8.89, which is highly significant. As is discussed in a later section, we think that most of the difference between return rates of sport and commercial tagged fish is caused by immediate tagging mortality. Immediate tagging mortality does not affect estimates of instantaneous total mortality. Therefore, we decided to use as much of the available data as possible and combined the data for estimates of mortality rates. Immediate tagging mortality does affect estimates of rates of exploitation and the components of mortality. Adjustments were made in an attempt to remove the effects of immediate tagging mortality and tag shedding.

Total Mortality Estimates – Chapman and Robson Method

Following the notation of Bayliff and Mobrand (1972), the number of tags remaining on bluefin at time t (years) is given by

$$N_t = N_0 \, \pi \rho e^{-Zt} \qquad (1)$$

where N_t = Number of tags remaining on bluefin at time t
N_0 = number of released tags
π = portion of bluefin which remain alive after Type-I, immediate, tagging mortality takes place
ρ = portion of tags which are retained after Type-I shedding takes place
Z = instantaneous total losses on an annual basis.

$$Z = F + X$$

where F = instantaneous fishing mortality on an annual basis
X = instantaneous other losses on an annual basis.

$$X = M + G + L + E$$

where M = instantaneous natural mortality on an annual basis
G = instantaneous Type-II tagging mortality on an annual basis
L = instantaneous Type-II tag shedding on an annual basis
E = instantaneous emigration from fishing grounds on an annual basis.

The number of tags returned during a year is given by

$$n_t = \frac{FcN_t}{Z} (1 - e^{-Z}) \qquad (2)$$

where n_t = number of tags returned between t and $t + 1$
c = portion of recovered tags that are returned.

Many assumptions are implicit in the above model. An exponential model is assumed to be correct. It is assumed that all instantaneous shedding, mortality, and emigration rates are constant—within years and among years. Since fishing was concentrated during the summer season, the assumption of constant fishing mortality is not valid. Also fishing effort probably varied over the years of the study. Available measures of fishing effort are thought to be inaccurate but were used in the last part of the analysis. The validity of the assumption of constant rate of emigration is not known, but tag returns suggest that transatlantic migrations are sporadic. This suggests that the assumption of constant emigration is not valid. While we recognize that some of our assumptions probably are invalid, it is our judgment that the effect of the violations on our results is not serious.

For the first part of the analysis we assumed that c, π, and ρ equal one. In the first analysis minimum variance unbiased estimates of the total annual survival rates were computed by the method developed by Chapman and Robson (1960) for the recovery data by year pooled in a variety of different ways over release categories. Confidence intervals were computed for s, the fraction surviving per year, and Z, the associated instantaneous mortality rate. A chi-square test was used to determine if the number of recaptures in the first recovery period is compatible with the survival pattern exhibited by the rest of the data, i.e., if the hypothesis of constant F and X is true. This test was applied sequentially, i.e., the second year was defined as the first recapture category and the test repeated until either all recapture years were eliminated or a survival rate was obtained from some subset of the data. For all releases the tagging year was taken as the first recapture category at the start of the analysis. The results of the survival rate computations are shown in Table 4 for the following data groupings:

1) Over all years
2) Over three adjacent release years
3) Individual years
4) July releases for three adjacent release years
5) Individual months within years
6) Release groups as defined in Table 1.

An obvious feature of this analysis is that in many of the recapture series, the numbers recovered the first year or two were higher than expected from the entire recapture series. This result is somewhat surprising because it might be expected that the number recaptured the first year would be underrepresented because of less exposure to the fishery. Three possible factors that could have caused the higher than expected recaptures in the first year or two after release are:

1) Tagged fish were released into an area where fishing activity was concentrated.
2) The proportion of the population migrating into the fishing area decreased as the fish became older; thus the availability of the tagged fish in the fishing area may have fallen off rapidly enough in later years to have caused a disproportionate number of recaptures in the first and second years after release.
3) The method of estimation assumes constant fishing mortality rates and other loss rates; variability in recovery effort could have caused the number of recaptures per year to deviate from a simple exponential decline with time.

Several aspects of the data emerge from Table 4. The estimates of survival rates are low but highly erratic; restricting the releases to finer time-location grids did not improve the stability of the estimates as might be expected. Since no time trend in survival is evident, pooling over years is a useful device to average out some of the fluctuations in the data. In one sense this is a substitute for use of recapture effort statistics and working with the number of recoveries per unit of recovery effort. The recaptures per year were combined over years using various weighting factors to develop adjusted numbers recaptured per year. None of these weighting schemes offered an improvement in the use of the simple unweighted average percent recapture per year at liberty for the years 1964-68. The proportion surviving per year as estimated from the simple average of the percentages was 0.188. This value is well within the confidence interval of the s-value of 0.231 estimated from the actual numbers pooled over all years. For the latter estimate, however, we did not use the recoveries made during the first 2 yr at liberty.

Inclusion of the first two recapture periods in the Chapman-Robson analysis, particularly for the last set of release groups which are fairly homogeneous, had the general effect of reducing the survival estimates. The numbers of recaptures

TABLE 4.—Survival rate estimates for various release group categories of tagged bluefin tuna.

Type of group[1]	Group	Recapture years used in s and Z computation	s(95% confidence interval)	Z(95% confidence interval)
1	All	[2](1, 2), 3, 4, 5	0.231 (.16, .30)	1.44 (1.14, 1.75)
[1]2	1963-65	-	Not constant (NC)	
	1964-66	[2](1, 2), 3, 4, 5	.174 (.09, .26)	1.70 (1.23, 2.16)
	1965-67	(1)[1], 2, 3, 4, 5	.118 (.10, .14)	2.13 (1.93, 2.32)
	1966-68	[2](1, 2), 3, 4, 5	.254 (.14, .37)	1.32 (0.88, 1.77)
	1967-69	[2](1), 2, 3, 4	.103 (.04, .17)	2.19 (1.60, 2.79)
	1968-70	-	NC	
3	1964	-	NC	
	1965	1, 2, 3, 4	.343 (.29, .39)	1.07 (.93, 1.21)
	1966	[2](1, 2), 3, 4, 5	.233 (.14, .32)	1.42 (1.03, 1.81)
	1967	(1)[1], 2, 3, 4	.323 (.24, .41)	1.11 (0.86, 1.37)
	1968	1, 2, 3	.243 (.17, .31)	1.39 (1.11, 1.68)
	1969		NC	
4	July 1963-65	1, 2, 3	.146 (.10, .19)	1.90 (1.61, 2.19)
	July 1964-66	[2](1, 2), 3, 4, 5	.400 (.20, .60)	0.87 (0.39, 1.34)
	July 1965-67	[2](1, 2), 3, 4, 5	.355 (.18, .53)	0.99 (0.51, 1.46)
	July 1966-68	[2](1, 2), 3, 4, 5	.367 (.19, .55)	0.96 (0.49, 1.42)
	July 1967-69	1, 2, 3, 4	.246 (.19, .30)	1.39 (1.17, 1.61)
	July 1968-70	-	NC	
[3]5	July 1964	1, 2	.128 (.06, .19)	2.00 (1.50, 2.49)
	Aug. 1964	-	NC	
	July 1965	1, 2, 3	.160 (.11, .21)	1.81 (1.48, 2.13)
	Aug. 1965	-	NC	
	July 1966	[2](1, 2), 3, 4, 5	.407 (.21, .60)	0.85 (0.40, 1.30)
	Aug. 1966	[2](1, 2), 3, 4, 5	.085 (.05, .12)	2.43 (2.08, 2.79)
	July 1967	1, 2, 3, 4	.244 (.18, .31)	1.39 (1.13, 1.66)
	Aug. 1967	-	NC	
	July 1968	1, 2, 3	.201 (.13, .27)	1.57 (1.23, 1.92)
	July 1969	-	NC	
	Aug. 1969	-	NC	
6	G1	1, 2, 3, 4	.582 (.45, .72)	0.53 (0.31, 0.75)
	G2A	1, 2	.189 (.06, .32)	1.57 (0.90, 2.24)
	G2B	1, 2	.065 (.00, .15)	2.45 (1.10, 3.79)
	G2C	1, 2	.160 (.01, .31)	1.68 (0.78, 2.58)
	3	-	NC	
	4A	1, 2, 3	.190 (.07, .31)	1.57 (0.95, 2.20)
	4B	1, 2, 3	.165 (.09, .24)	1.75 (1.30, 2.21)
	4C	1, 2	.083 (.00, .18)	2.27 (1.18, 3.36)
	5A	-	NC	
	5B	-	NC	
	5C	-	NC	
	6A	-	NC	
	6B	-	NC	
	6C	-	NC	
	6D	-	NC	
	6E	-	NC	
	7A	-	NC	
	7B	[2](1, 2), 3, 4, 5	.375 (.01, .74)	0.88 (0.04, 1.71)
	7C	[2](1), 2, 3, 4	.083 (.01, .16)	2.34 (1.49, 3.19)
	7D	-	NC	
	7E	-	NC	
	7F	-	NC	
	7G	-	NC	
	8	[2](1), 2, 3, 4	.125 (.00, .26)	1.88 (0.83, 2.94)
	9A	1, 2	.154 (.01, .30)	1.72 (0.82, 2.62)
	9B	1, 2, 3, 4	.205 (.13, .28)	1.55 (1.19, 1.92)
	10	-	NC	
	11A	1, 2, 3	.357 (.17, .54)	0.98 (0.48, 1.47)
	11B	1, 2, 3	.240 (.12, .36)	1.37 (0.87, 1.87)
	12	-	NC	
	13	-	NC	
	14	-	NC	

[1] Includes tags assigned by cruise number.

[2] Recapture years eliminated by chi-square test of full recruitment to tagged population are shown in parentheses.

[3] July results include tags assigned by cruise number.

dropped off so rapidly, however, after the first two recapture periods that little reliability can actually be placed on estimates using only data from the tail end of the time series.

This first examination of the recaptures by time at liberty was followed by a revised analysis of the July releases each year and all releases each year for 1964 through 1968. An attempt to include all tags in the analysis was made by assigning tags without recorded release dates to most likely release dates by means of the accompanying information, e.g., by cruise number. For the most part this revision produced minor changes in the estimates of total survival rates. Raw exploitation rates were estimated from the total number of recaptures per release using all data whether or not any information was available on date of recapture.

Estimates of Fishing and Other Losses

We used the following equations to estimate rates of exploitation, fishing, and other losses:

$$\hat{u}_T = R/N_0$$

where $\hat{u}_T$ = estimate of total exploitation of tagged bluefin tuna over n years

R = number of tag returns.

$$\hat{u}_1 = \hat{u}_T / \sum_{i=0}^{n} \hat{s}^i$$

where $\hat{s}$ = survival rate estimated from revised data by the Chapman-Robson method

$\hat{u}_1$ = estimate of single season exploitation of tagged bluefin tuna.

$$\hat{F} = \hat{u} \ (-\ln \hat{s})/(1 - \hat{s})$$

$$\hat{X} = \ln(\hat{s}) - \hat{F}$$

These estimates for July releases are shown in Part A of Table 5, and in Part B of the same table, estimates of the same set of parameters for all releases are given with the exception of the single season exploitation rates. We believe that distributing the releases during the entire fishing season, rather than restricting them to the first part of the season, July, makes it impossible to estimate a single season exploitation rate. It will be noted that the actual observed exploitation rates are high, especially in view of the fact that no corrections were made for either immediate tagging mortality, tag shedding, or nonreporting. The total recapture percentages range from 16% to 48%.

Lenarz et al. (1973) estimated that the rate of immediate tag shedding $(1 - \rho)$ for Atlantic bluefin tuna is 0.027 and that the instantaneous rate of tag shedding (L) is 0.310. Their estimates were used to correct our estimates of exploitation and mortality rates for shedding as follows:

TABLE 5.—Estimates of total survival, rate of exploitation, fishing mortality rate and total other loss rate of tagged bluefin tuna for July releases and for all releases by year of release.

Item	1964	1965	1966	1967	1968
Part A. July releases only:					
(N) Numbers released	397	951	2,047	448	226
(R) Numbers recovered	96	169	461	131	108
$\hat{s}$	0.128	0.160	0.407	0.244	0.201
$\hat{u}_1$	0.211	0.150	0.143	0.224	0.385
$\hat{u}_T$	0.242	0.178	0.225	0.292	0.478
$\hat{F}$	0.497	0.327	0.217	0.418	0.773
$\hat{X}$	1.558	1.506	0.697	0.999	0.838
$(\hat{F} + \hat{X})$	2.056	1.833	0.899	1.411	1.604
Part B. All releases by year:					
(N) Numbers released	465	1,672	3,959	628	260
(R) Numbers recovered	132	262	1,177	187	116
$\hat{s}$	0.196	0.343	0.233	0.323	0.243
$\hat{u}_T$	0.284	0.157	0.297	0.298	0.446
$\hat{F}$	0.463	0.168	0.433	0.337	0.631
$\hat{X}$	1.167	0.902	1.024	0.793	0.784
$(\hat{F} + \hat{X})$	1.630	1.070	1.457	1.130	1.415

$$(\hat{F} + \hat{X})^* = \hat{F} + \hat{X} - L$$

where $(\hat{F} + \hat{X})^*$ = estimate of total instantaneous apparent mortality corrected for tag shedding rate,

$$\hat{s}^* = e^{-(\hat{F} + \hat{X})^*}$$

where $\hat{s}^*$ = estimate of annual survival corrected for shedding rate,

$$\hat{u}_T^* = \hat{u}_T/\hat{\rho}$$

where $\hat{u}_T^*$ = estimate of total exploitation of tagged bluefin tuna corrected for immediate tag shedding,

$$\hat{u}_1^* = \hat{u}_1/\hat{\rho}$$

where $\hat{u}_1^*$ = estimate of seasonal exploitation corrected for immediate tag shedding,

$$\hat{F}^* = \hat{u}_1^* \ (-\ln s)/(1 - \hat{s})$$

where $\hat{F}^*$ = estimate of F corrected for immediate tag shedding,

$$\hat{X}^* = -\ln(\hat{s}^*) - \hat{F}^*$$

where $\hat{X}^*$ = estimate of X corrected for immediate tag shedding,

$$\hat{u}_1^{**} = \frac{\hat{F}^*}{\hat{F}^* + \hat{X}^*} \ (1 - \hat{s}^*)$$

where $\hat{u}_1^{**}$ = estimate of single season exploitation of tagged and untagged bluefin corrected for all tag shedding, and

$$\hat{u}_T^{**} = \hat{u}_1^{**} \sum_{i=0}^{n} (\hat{s}^*)^i$$

where $\hat{u}_T^{**}$ = estimate of total exploitation of tagged and untagged bluefin corrected for all tag shedding.

The estimates are shown in Table 6. Estimates of $\hat{X}^*$ (other losses) range from 0.366 to 1.234 (average = 0.792). The estimates of $\hat{X}^*$ are considerably higher than expected values of M (natural mortality) for bluefin. Bluefin are very long-lived fish and values of M of 0.1 to 0.2, if M is constant, would seem reasonable. Thus, there may be significant amounts of Type-I (immediate) and Type-II (long-term) tagging mortality, nonreporting, and/or apparent mortality caused by emigration.

TABLE 6.—Estimates of rates of exploitation and mortality of bluefin tuna corrected for tag shedding.

Item	1964	1965	1966	1967	1968
$(\hat{F} + \hat{X})^*$	1.746	1.523	0.589	1.101	1.294
$\hat{s}^*$	0.174	0.218	0.555	0.333	0.274
$\hat{u}_T^*$	0.249	0.183	0.231	0.300	0.491
$\hat{u}_1$	0.217	0.154	0.147	0.230	0.396
$\hat{F}^*$	0.512	0.336	0.223	0.429	0.795
$\hat{X}^*$	1.234	1.187	0.366	0.671	0.499
$\hat{u}_1^{**}$	0.242	0.172	0.168	0.260	0.446
$\hat{u}_T^{**}$	0.284	0.218	0.342	0.388	0.611

It seems plausible that some Type-I tagging mortality exists. In an earlier section it was noted that, more returns were obtained from sport gear releases than from commercial gear releases. Statistically significant, more returns were obtained from sport releases than commercial releases in 1965, 1966, 1969, and 1970. A possible cause of the difference in return rates could be that sport tagged bluefin are of different ages than commercially tagged bluefin. Bluefin of different ages could suffer different rates of tagging mortality and shedding, and could behave differently. Data have not been compiled in a fashion that allows examination of the age at release by the two gear types. We recommend that it be and assume for the present that age-dependent effects are negligible. The differences in return rates could also be caused by Type-I tagging mortality. Experienced taggers report that sport-gear-caught bluefin appear to be in better condition than those caught by commercial gear. Also, commercial gear tends to capture entire schools of bluefin while sport gear captures one bluefin at a time. Thus, bluefin released from sport gear tend to be released into the immediate area of a school of bluefin while bluefin released from commercial gear are not. There may be an advantage for bluefin to be in a school. Bayliff (1973) found that return rates of purse-seine-caught yellowfin tuna tagged immediately after a set is made can be more than two times higher than yellowfin tagged at a later time (Table 7). This evidence suggests that Type-I tagging mortality is very important

TABLE 7.—Releases, returns, and percentages of return of yellowfin tuna for IATTC[1] Cruise 1055, by time between commencement of tagging and release of fish (from Bayliff, 1973).

Time (min)	Number released	Number returned	% returned
0-10	1,920	277	14.4
10-20	1,972	195	9.9
20-30	1,563	86	5.5
30-40	1,145	47	4.1
40-50	934	44	4.7
>50	975	23	2.4
Total	8,509	672	7.9

[1]Inter-American Tropical Tuna Commission.

for purse-seine-caught yellowfin tuna. Bayliff[6] (pers. commun.) believes that bluefin tuna are more hardy than yellowfin tuna and thus expects that Type-I tagging mortality is lower for bluefin than for yellowfin.

Assuming that sport releases suffered insignificant amounts of Type-I tagging mortality and using the Mantel-Haenszel weighting procedure, the 1964-68 average Type-I tagging mortality for commercial tagged fish was 21%. During this period, 96% of the releases were commercial tagged fish. The average Type-I tagging mortality for all releases during 1964-68 was 20%.

The rates of exploitation and mortality were corrected for Type-I tagging mortality as follows:

$$\hat{u}_T^{***} = \hat{u}_T^{**}/\pi$$

where $\hat{u}_T^{***}$ = estimate of total exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{u}_1^{***} = \hat{u}_1^{**}/\pi$$

where $\hat{u}_1^{***}$ = estimate of seasonal exploitation corrected for shedding and Type-I tagging mortality,

$$\hat{F}^{**} = \hat{u}_1^{***}(-\ln \hat{s}^*)/(1 - \hat{s}^*)$$

where $\hat{F}^{**}$ = estimate of F corrected for shedding and Type-I tagging mortality, and

$$\hat{X}^{**} = -\ln(\hat{s}^*) - \hat{F}^{**}$$

where $\hat{X}^{**}$ = estimate of X corrected for shedding and Type-I tagging mortality.

The estimates are shown in Table 8. The values of $\hat{X}^{**}$ range from 0.300 to 1.109 (average = 0.678) and are still higher than the expected rate of natural mortality for bluefin. The large difference between values for 1964-65 and the values for 1966-68 is worth noting. Food and Agriculture Organization (1972) reports that a relatively large number of bluefin tuna tagged in the northwest Atlantic in 1965 were recovered in the Bay of Biscay during the following year. This suggests that a large-scale transatlantic migration occurred between the 1965 and 1966 fishing seasons. Thus migration from the fishery is a plausible explanation for a portion of $\hat{X}^{**}$.

TABLE 8.—Estimates of rates of exploitation and mortality for northwest Atlantic bluefin tuna. The rates have been corrected for tag shedding and a hypothetical value of Type-I tagging mortality.

	1964	1965	1966	1967	1968	Average
u_T^{***}	0.355	0.272	0.428	0.485	0.764	[1]0.456
u_1^{***}	0.302	0.215	0.210	0.325	0.558	[1]0.327
F^{**}	0.639	0.419	0.278	0.536	0.995	0.573
X^{**}	1.110	1.104	0.311	0.564	0.300	0.678

[1]Calculated from averages of F^{**} and X^{**}.

Total Mortality Estimates – Regression Method

We next used available effort data for examining the effect of changes in effort on our estimates of mortality. The effort data were obtained from inquiries and logbooks of purse seiners that participated in the commercial fishery for bluefin in the northwestern Atlantic. The data have not been standardized by vessel class. We question the validity of the data as a measure of fishing effort, i.e., proportional to F, because a varying portion of the fleet relied heavily on airplane scouting. Conversion of the data to a standard unit of effort is worth a study in itself and we recommend that such a study be carried out.

In another attempt to estimate total mortality the natural logarithm of the number of returns per unit effort (Table 9), taking the number of boat-days recorded per season as a legitimate measure of effort, was regressed on time as measured to the center of each year following the release. An exact

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[6] Bayliff, W. H. Inter-Am. Trop. Tuna Comm., P. O. Box 271, La Jolla, CA 92037.

TABLE 9.—Returns of tagged bluefin tuna per boat-day by years at liberty.

Year	0	1	2	3	4
Part A. July releases only:					
1964	0.0902	0.0344			
1965	0.3538	0.0968	0.0374		
1966	0.9839	1.3957	0.1059	0.0526	0.0111
1967	0.5080	0.3647	0.0421	0.0037	
1968	1.0235	0.1579	0.0222		
Part B. All releases:					
1964	0.1100	0.0786			
1965	0.4029	0.3280	0.1925	0.0718	
1966	2.8495	3.1016	0.6235	0.0842	0.0222
1967	0.5241	0.7059	0.1684	0.0481	
1968	1.0353	0.2000	0.0333		

analytical formulation of this mortality model has two independent variates—cumulative time and cumulative effort. Not only are these two variables so highly correlated that it is virtually impossible to obtain useful estimates of the two regression coefficients, but also there are too few data points available for multiple regression analysis. The regression coefficient of the simple cumulative time regression is a crude measure of the total mortality rate. The fitted regression lines are shown in Figure 3 for July releases and in Figure 4 for all releases for each year. The values of the coefficients are given in Table 10.

With the exception of 1966, when the returns per boat-day increased during the year following release (and the data were eliminated from the regression), the logarithms of the recaptures per unit effort decrease in a linear fashion and it is clear the regressions provide reasonable fits to the data points. Seven of the eight estimated survival rates shown in Table 10 are lower than their counterparts in Table 5. Both of these analyses provide at best only crude approximations of the true survival rates; however, they do show fair general agreement. The catch-per-effort estimates indicate the loss rates are tending to increase with time.

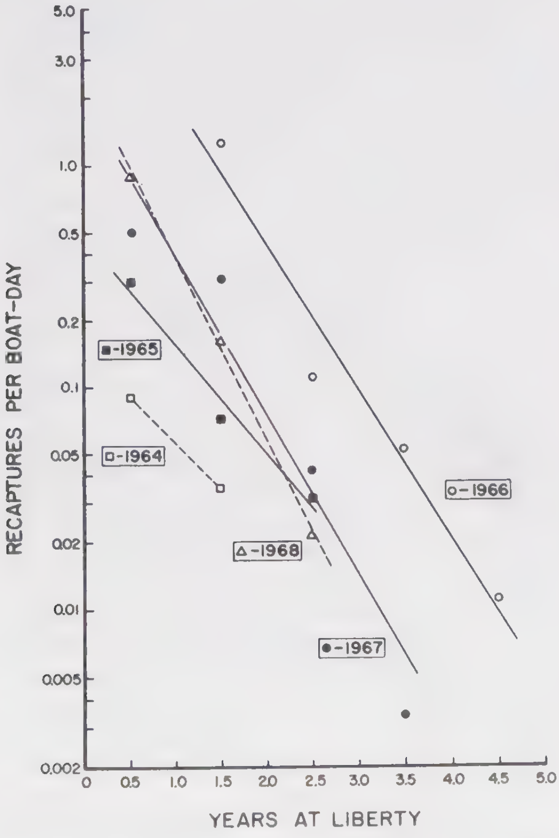

FIGURE 3.—Regression of recaptures per boat-day vs. time at liberty for July releases of tagged bluefin tuna.

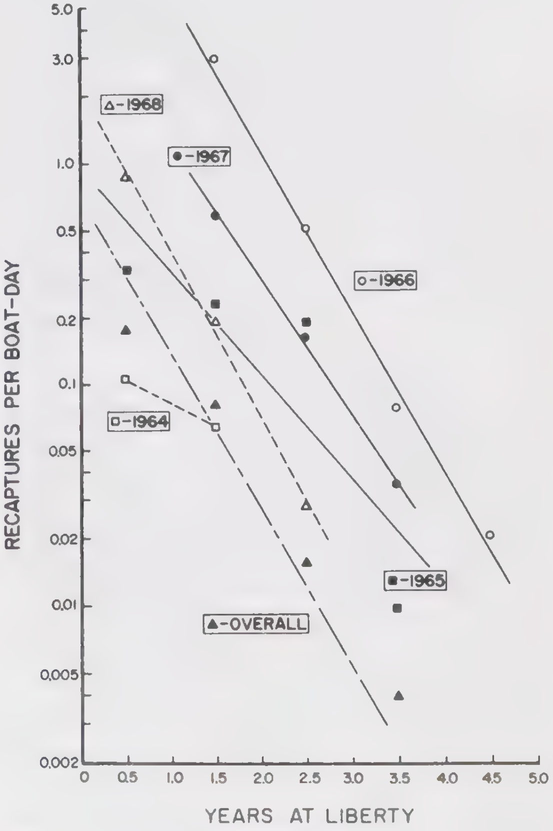

FIGURE 4.—Regression of recaptures per boat-day vs. time for all releases, by year, of tagged bluefin tuna.

TABLE 10.—Estimates of total survival rates of tagged bluefin tuna from regression analysis of return per unit-of-effort data.

Year	July releases only		All releases	
	Z	s	Z	s
1965	1.12	0.33	1.08	0.34
1966[1]	1.51	0.22	1.68	0.19
1967	1.70	0.18	1.41	0.24
1968	1.87	0.15	1.73	0.18
Average[2]	1.55	[3]0.21	1.48	[3]0.23

[1] Recaptures in release year not included in 1966 regression analysis.

[2] Regression estimates using average unweighted percentage returns for 1964-68 are: $Z = 1.67$ and $s = 0.19$. This estimate happens to be exactly the same as the estimate of $Z = 1.67 = (\text{average time at liberty})^{1}$ where average time at liberty is 0.60 yr.

[3] Survival rate computed from average Z-value.

DISCUSSION

Exactly what these "survivals" are measuring is of prime interest. They are properly thought of as the results of disappearance rates which are composed of mortalities (*F, M,* and *G),* tag shedding, and changing migratory patterns with age. Apparently few of the older fish entered the surface fishery in the western north Atlantic during the period of the study and the decreasing proportion of the population that entered the fishery is a primary factor lowering the apparent survival. In 1966 when the fish tagged were significantly younger than in the other years—having an average age of 1.4 yr as opposed to average ages of at least a year older in other tagging years—the greatest return of tags occurred during the year after release. For these younger bluefin, a higher proportion returned to the fishing area the year after they were released than for the older tagged fish.

The exploitation rate on the tagged fish was exceedingly high when they were in the fishery. The high fishing mortality rates in Table 8 may underestimate the true rates for tagged bluefin; most of the various sources of error that may bias these estimates act to decrease the estimate of the fishing rate relative to its true value. However, it is known that bluefin available to the northwest Atlantic fisheries are not a closed population. Tagging studies have revealed transatlantic migrations to and from the fishery. Migration could also occur from the middle Atlantic. Thus it must still be determined whether the high exploitation rate applied to the population or just to the portion of the population that entered the fishery. Ricker (1958:35) describes the effects of tagging fish that are more vulnerable to fishing than other members of the population. "Again, if fish of certain sizes are more vulnerable than others, a Peterson tagging experiment is apt to overemphasize the vulnerable ones both in respect to tags put out and recaptures made; hence the estimate of rate of exploitation is too high and the population estimate is too low." Future analysis stratifying the data by age at release would help to answer some questions that arise because of the migratory behavior of bluefin. We suggest cohort analysis in the fashion of Bayliff (1971) as a productive method of analysis.

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Skipjack Tuna, *Katsuwonus pelamis*, Underutilized Resource

TER M. MATSUMOTO

ODUCTION

e tunas are the most important
e large fishes constituting the
ited pelagic resources of the
oceans. The largest catches of
, including the yellowfin tuna,
nus albacares; the bigeye tuna,
esus; the bluefin tuna, *T. thynnus;*
southern bluefin tuna, *T. mac-*
; and the albacore, *T. alalunga,*
aken with deep-fishing longline
in the pelagic waters of non-
al areas. The skipjack tuna,
wonus pelamis, is taken at the
ce, mostly with purse seine and
and-line gear. It is also taken
ntally with the longline. Skip-
una constitutes about 30 percent
total tuna catch, and in recent
has come to replace the yellow-
na as the dominant species.

cent studies of longline catches
ate that, except for the bigeye
in the Atlantic and possibly the
ore in the South Pacific, all the
taken with the longline are now
exploited at or near their maxi-
sustainable yields in the Atlan-
Pacific, and Indian Oceans (Roths-
d and Uchida, 1968; Kikawa et al.,
8; Hayasi et al., 1970; Suda, 1971;
Skillman[1]). The skipjack tuna is
only species of tuna presently ex-
ited in large commercial quantities
can withstand large increases in
ing pressure. Unlike most other
as that are caught in large quanti-
in midocean areas, the bulk of the
jack tuna is generally taken in
waters associated with land masses. Yet its occurrence in tropical and subtropical areas far removed from land, as evidenced by incidental catches on the longline gear, demonstrates that the species is not fully exploited, despite the tremendous increase in fishing in recent years in the western equatorial Pacific.

FISHERIES AND DISTRIBUTION OF FISH

The catch statistics (FAO, 1966, 1972) show that in the most recent 6 years, 1966-71, the annual world production of skipjack tuna has been maintained at the 300,000-350,000 metric ton (MT) level, up from roughly 200,000-250,000 MT in years prior to 1966 (Table 1). The total catch appears low, probably due to incomplete reporting of catches from areas that have expanded rapidly in the last few years. A most obvious discrepancy is noted in the catch from the Indian Ocean. The catches for 1970 and 1971 are given as 100 MT, but according to Sivasubramaniam (1972) catches of skipjack tuna there have increased rapidly since 1969, and at present about 45,000-50,000 MT are taken from this ocean. A recent summary of the world's catch of skipjack tuna for 1971 by Joseph (in press) shows an even greater discrepancy; his estimated total of 438,000 MT exceeds that of the FAO statistics by 108,000 MT. Joseph's breakdown of the total catch by oceans shows 82,000 MT from the Atlantic, 39,000 MT from the Indian, and 317,000 MT from the Pacific. In all three oceans his catch estimates exceed the totals of the FAO statistics.

Despite these discrepancies, the FAO records are useful for determining long-term catch trends. The catch records (Table 1) reflect the fact that skipjack tuna is fast becoming, if it is not already, the dominant species in the catches of tunas. Prior to 1966 the yellowfin tuna dominated the catch, but in the 6 years beginning in 1966, skipjack tuna has dominated the world catch in 3 and possibly 4 years. Joseph's estimates for 1971 show that the skipjack tuna catch exceeded that of yellowfin tuna by 130,000 MT.

Up to recent years, the major skipjack tuna fisheries were concentrated in only a few places in the Pacific Ocean; the U.S. fishery in the eastern Pacific off the coasts of Baja California, Central America, and northern

Table 1.—Annual landings (in 1,000 metric tons) of skipjack tuna from the major oceans (FAO, 1966, 1972).

	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
Atlantic Ocean	0.3	0.3	2.2	1.4	10.0	10.4	13.0	24.3	18.3	34.7	36.0
Northwest	No breakdown by area				0.0	0.0	0.0	1.8	0.4	0.7	1.5
Western central					1.0	1.0	1.1	1.7	1.2	1.4	1.5
Eastern central					7.1	6.0	8.4	15.8	14.4	31.6	32.0
Southwest					0.5	0.6	1.5	0.8	0.4	0.0	0.0
Southeast					1.4	2.8	2.0	4.2	1.9	1.0	1.0
Indian Ocean	—	—	—	—	0.1	0.1	0.2	0.3	0.3	0.1	0.1
Western	No breakdown by area				0.1	0.1	0.2	0.2	0.2	0.1	0.1
Eastern					0.0	0.0	0.0	0.1	0.1	0.0	0.0
Pacific Ocean	219.0	252.4	200.8	226.5	237.4	310.1	337.4	275.1	271.1	288.5	294.0
Northwest	No breakdown by area				145.8	208.4	176,0	147.6	163.1	166.2	206.8
Northeast					0.2	—	0.1	—	0.1	0.2	0.3
Western central					—	35.7	35.2	42.3	41.5	53.6	0.7
Eastern central					76.2	54.1	106.9	74.4	51.4	58.3	79.0
Southwest					1.6	1.6	1.7	1.9	1.6	1.5	1.5
Southeast					13.6	10.3	17.5	8.9	13.4	8.7	5.7
Total	219.3	252.7	203.0	227.9	247.5	320.6	350.6	299.7	289.7	323.3	330.1

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fishery and its potential for expan-
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South America, the northwestern Pacific fishery, which includes the fisheries off Japan, Formosa, and Ryukyu Islands, and the Japanese southern water fishery in the western equatorial Pacific. Between 1965 and 1970 the northwestern Pacific fishery contributed annually 147,000-208,000 tons to the world catch, the Japanese southern water fishery contributed 35,000-54,000 tons and the American fishery (excluding Hawaii) contributed 64,000-124,000 tons (Table 1). Since 1970 two more areas, Sri Lanka (Ceylon)-Laccadive-Maldive Islands in the Indian Ocean and the eastern equatorial Atlantic, have developed into significant fisheries, the latter contributing more than 32,000 tons. Together, these five areas contributed slightly more than 97 percent of the total world catch in 1970 and 1971.

A small-scale commercial skipjack tuna fishery dating back to the early 1900's exists in the Hawaiian Islands (June, 1951). This fishery produces about 4,600 tons per year (Rothschild and Uchida, 1968). Other small-scale fisheries in the Pacific Ocean are situated in Tahiti, where as much as 730 tons were taken in 1966 (Brun and Klawe, 1968), and in New Caledonia (Rothschild and Uchida, 1968). More recently the Japanese have begun to expand their pole-and-line fishing operations into the southwestern Pacific, particularly in the New Guinea-Solomon Islands area. With as many as 19 boats operating at any one time in the Bismarck Sea (New Guinea), the 1971 catch of skipjack tuna totaled 16,860 MT (Kearney, 1973).

Although the major skipjack tuna fisheries are concentrated in a few places, the species is widely distributed in all oceans. It has been taken as an incidental catch on the tuna longline as far north as lat.40°N in the western part of both the Atlantic and Pacific Oceans, as far south as lat.40°S in the western part of the Indian and Pacific Oceans, and as far south as lat.40°S in the Atlantic Ocean (Fig. 1). Longitudinally, it has been taken continuously across the breadth of both the Indian and Pacific Oceans.

BIOLOGY AND ECOLOGY

Until recent years little fishing for skipjack tuna was done in the Atlantic and Indian Oceans. Consequently, research on the species and resource has been virtually limited to that in the Pacific Ocean.

It is now known that skipjack tuna begin spawning when they are about 40 cm long, and that each fish spawns between 100,000 and 2,000,000 eggs per spawning (Yoshida, 1966). The number of eggs spawned varies greatly with size of fish and even among fish of the same size. Spawning generally occurs throughout the year in tropical waters, but only in the warm seasons (late spring to early fall) in subtropical waters. Although spawning is greatly influenced by warm water and most skipjack tuna larvae are found in waters with surface temperature above 24°C, it is not uncommon to find them in waters below 23°C. Data collected by the Honolulu Laboratory, National Marine Fisheries Service, indicate the lowest temperature in which skipjack tuna larvae were found was 22.1°C. The larvae of skipjack tuna are distributed widely in all three oceans (Ehrenbaum, 1924; Klawe, 1960; Richards, 1969; Ueyanagi, 1969, 1971), but more so in the Pacific than in the others (Fig. 1). The distribution of larvae is narrowed latitudinally in the east and greatly expanded in the west, reflecting the response of spawning to warm water. In spite of their wide latitudinal range in the western and part of the central Pacific, most of the larvae are found in equatorial waters west of long.145°W between lat.20°N and 10°S. To the east of long.145°W the band of heavy concentration of larvae is even narrower, between lat.10°N and 10°S. The principal spawning area along this band is located in the central Pacific between long.150°E and 150°W (Fig. 2).

Although there have been a number of studies on age and growth of the skipjack tuna, only a few have attempted to assign ages to specific size groups (Aikawa and Kato, 1938; Brock, 1954; Schaefer, 1960; Yokota et al., 1961; Kawasaki, 1965; and Yoshida, 1971). Of these, even fewer agree as to the size of fish at age 1 and above age 4. The closest to an agreement is noted in fish of ages 2 and 3 (fish of 45-52 cm and 63-67 cm, respectively), which make up the bulk of the commercial catch. Prior to

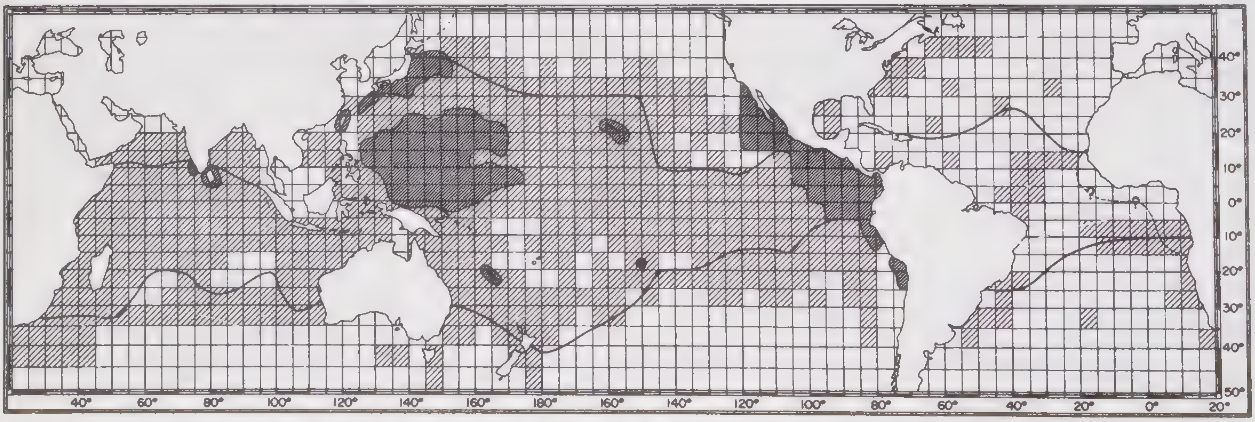

Figure 1.—Areas of present skipjack tuna fisheries (dark shaded) and areas where skipjack tuna were taken incidentally on longline gear (light shaded) by the Japanese in the years 1969-71 (Fisheries Agency of Japan, 1971, 1972, 1973). The broken line off western Africa represents the estimated boundary of the eastern Atlantic skipjack tuna fishery. The northern and southern boundaries of larval skipjack tuna distribution are shown by solid lines.

their entry into the various fisheries, the young, after having spent some time within the spawning grounds, gradually spread out. (Kawasaki [1965, 1972] gives a detailed summary of the movement of skipjack tuna by age groups.) By the time the skipjack tuna have attained age 2, they have reached their widest distribution: in the west into waters off northern Japan; in the east into waters off Central America; off Baja California to the north, and northern Chile to the south. In the western Pacific these fish retreat south in the winter to spawn and return to the north as age 3 fish in the following summer. Only a small portion of older fish return north in subsequent years. In the eastern Pacific the age 2 fish make up the bulk of the fishery. These fish return to the central Pacific spawning grounds and, based on size distribution figures in Broadhead and Barrett (1964), probably reappear in the fishery as age 3 fish, off Mexico and Revilla Gigedo. A somewhat different situation exists in the central North Pacific. In waters around the Hawaiian Islands fish in their fourth year (72-84 cm) are taken in most years and these fish make up 40-80 percent of the catch during the peak fishing months, June-August (Rothschild, 1965). Equally large skipjack tuna are taken also in waters of the Marquesas and Society Islands (Rothschild and Uchida, 1968).

The northward and southward expansion of the skipjack tuna distribution follows a regular seasonal cycle (Matsumoto[2]). In both northern and southern hemispheres maximum poleward movement of fish occurs in their respective summer-fall season. In addition to this north-south seasonal movement the skipjack tuna also move along with the prevailing ocean currents (Fig. 3), foraging on organisms that are being transported therein. The combination of these two movements thus produces a roughly circular path, so that the resultant movement of skipjack tuna is counterclockwise in the South Pacific and clockwise in the North Pacific, except in the eastern part where it is counterclockwise (Fig. 4), similar to the current flow around the North Pacific Equatorial Water mass. Although Matsumoto's study was based on catches made with the longline, a gear that normally takes the larger and deeper-swimming tunas, the results are applicable to surface caught skipjack tuna, since the longline gear is capable also of taking skipjack tuna as small as 45 cm, the modal size common to most of the surface fisheries.

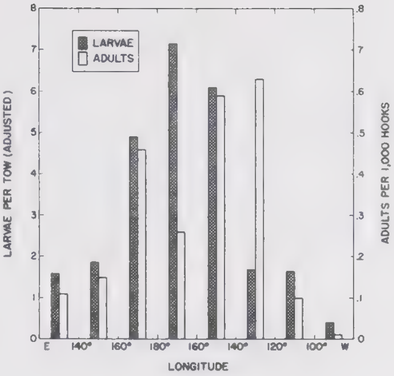

Figure 2.—Larval and adult skipjack tuna abundance across the Pacific Ocean between lat.20°N and 10°S (from Matsumoto[2]).

Before proceeding with resource assessment it is important that the population structure of the skipjack tuna be reviewed. Fujino (1970, 1972) has concluded, on the basis of serological studies, that in the Pacific Ocean a western subpopulation of skipjack tuna exists in both the northern and southern hemispheres west of a line running from southeastern Japan through the Bonin, Mariana, Marshall, and Gilbert Islands, between New Hebrides and Fiji Islands, and between Australia and New Zealand; and that this subpopulation is genetically distinct from the central-eastern Pacific subpopulation(s) to the east of this line. Fujino further noted that although both types of fish are found in Japanese waters, fish of the western subpopulation depart from the area within a few days of the entry of fish of the eastern-central Pacific subpopulation in September. This has been corroborated by length-frequency data showing two groups of 2-year-old skipjack tuna appearing in southeastern Japan during August (Kawasaki, 1972) with modal lengths differing by 5 to 6 cm.

It is not unlikely that the movement patterns shown in Figure 4 represent movements of stocks of skipjack tuna. The two westernmost stocks, one each in the northern and southern hemispheres, clearly belong to the western subpopulation and all other stocks to the east are of the eastern-central subpopulation. The intersecting of movement patterns from one stock to the next in the central and eastern Pacific gives rise to the thought that the progeny, if not the adults, could move from east to west in the northern hemisphere and from west to east in the southern hemisphere (Matsumoto[2]). Matsumoto has also shown that the skipjack tuna can move back and forth across the North Equatorial Countercurrent.

RESOURCE ASSESSMENT

Several estimates have been made of the potential yield of skipjack tuna in the Pacific Ocean. With the present state of knowledge about the parameters governing the dynamics of skipjack tuna populations, the estimates obtained thus far must be considered tentative and should be used with great caution. The pitfalls in such preliminary estimates are numerous, the most dangerous being that once an estimate is made, "it tends to stand by itself" (Kawasaki, 1972), and may be quoted out of context and become accepted as fact without reference to the author's qualifying assumptions and conditions. Such has been the fate of the estimates given by Rothschild (1966) and the Japan Fisheries Agency. The latter is summarized in Kawasaki (1972). Let us examine some of these.

Rothschild (1966), using the Beverton-Holt method, estimated the yield potential of skipjack tuna in the central Pacific Ocean. His estimates represented the potential yield of the escapement stock (fish that leave the fishery) of the eastern Pacific fishery in the event that the fishery continued to harvest these fish during their return to the central Pacific. He gave two estimates, one computed for a sojourn time of 2 months (sojourn time was defined as the time a fish spends in the fishing area), which he obtained from tag returns and which he considered rather short, and the other for a more conservative sojourn time of 6 months, selected arbitrarily. The first estimate was a fivefold to seventeenfold increase in yield and the second a twofold to sixfold increase. Using 70,000 tons as the annual average, these estimates correspond to increased annual catches of from 350,000 to 1,200,000 tons and from 140,000 to 420,000 tons.

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[2] Matsumoto, W. M. In preparation. Distribution, relative abundance, and movement of skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean based on Japanese tuna longline catches, 1964-67. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

Silliman (1966), employing a population-simulation method to the eastern Pacific fishery catch data, estimated a maximum yield of 225,000 tons, an increase of 155,000 tons or about twice the annual average catch. This estimate falls within the range of Rothschild's estimates based on a 6-month sojourn time. However, as noted by Rothschild, since the escapement stock almost certainly mixes with skipjack tuna that never circulate through the eastern Pacific fishery area, the estimates of yield must be highly conservative. This would apply also to Silliman's estimate.

The Japanese have come up with various estimates of potential yields of skipjack tuna for the Pacific as well as the Atlantic and Indian Oceans.

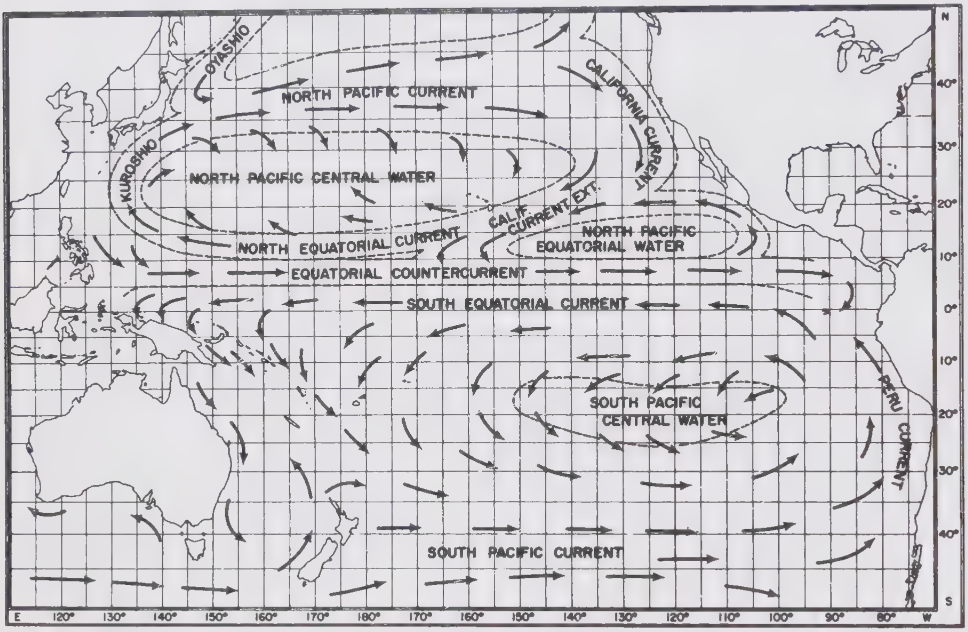
OYASHIO
NORTH PACIFIC CURRENT
CALIFORNIA CURRENT
KUROSHIO
NORTH PACIFIC CENTRAL WATER
CALIF. CURRENT EXT.
NORTH EQUATORIAL CURRENT
NORTH PACIFIC EQUATORIAL WATER
EQUATORIAL COUNTERCURRENT
SOUTH EQUATORIAL CURRENT
SOUTH PACIFIC CENTRAL WATER
PERU CURRENT
SOUTH PACIFIC CURRENT
N
40°
30°
20°
10°
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Figure 3.—Schematic diagram of the principal currents and water masses in the Pacific Ocean (from Matsumoto[2]).

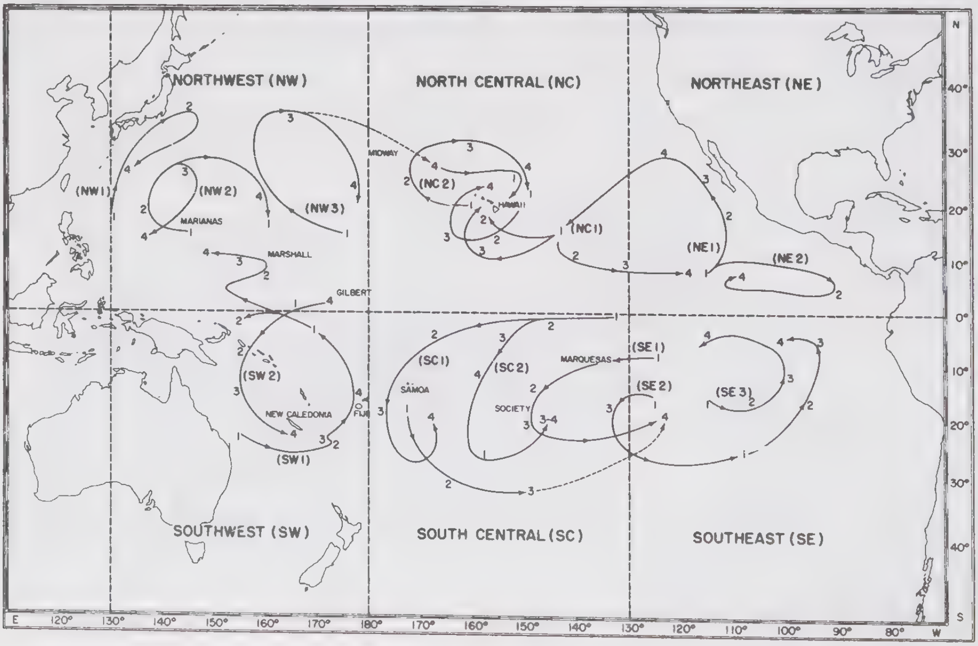
NORTHWEST (NW)
NORTH CENTRAL (NC)
NORTHEAST (NE)
(NW1)
(NW2)
(NW3)
MARIANAS
MIDWAY
(NC2)
HAWAII
(NC1)
MARSHALL
(NE1)
(NE2)
GILBERT
(SW2)
NEW CALEDONIA
FIJI
(SW1)
(SC1)
SAMOA
(SC2)
SOCIETY
MARQUESAS
(SE1)
(SE2)
(SE3)
SOUTHWEST (SW)
SOUTH CENTRAL (SC)
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Figure 4.—Assumed movement of the various stocks of skipjack tuna in the Pacific Ocean. The numerals along the migratory routes represent quarters and locations of high catch-per-effort cells of skipjack tuna taken by the Japanese longline fishery, 1964-67. Stock designations are shown in parentheses.

According to Kawasaki (1972), the estimated yields published by the Japan Fisheries Agency are as follows:

Area	1,000 tons
Japanese coastal	Increase of 200-400
Entire Pacific	Increase to 1,000
Indian Ocean	200-300
North Atlantic	100
South Atlantic	100-150

The author of these estimates is not known; however, in 1971 Akira Suda, Far Seas Fisheries Research Laboratory, Shimizu, Japan, in commenting on his estimate of potential production of skipjack tuna in the Pacific Ocean of between 800,000 and 1,000,000 tons, explained the method used in arriving at his estimate (excerpts from talk given at the June 1971 Conference of the Japan Fisheries Resources Convention Association. *In* Kawasaki, 1972.). He based his estimate on the premise that since from 1.7 to 1.8 times more skipjack tuna larvae were taken than larvae of other tunas, the spawning stock of skipjack tuna was also from 1.7 to 1.8 times (rounded off to 2) that of other tunas, and that therefore the potential production of skipjack tuna should be 2 times 400,000-500,000 tons, the production of other tunas. The method used to obtain 1 and 2 above could be similar to this.

The conclusion that the skipjack tuna yield should be twice that of all other tunas because there are twice as many skipjack tuna larvae seems to be an oversimplification of a complex conversion. If we look at the various factors permitting such a conversion, we find that this 2:1 ratio advantage in favor of the skipjack tuna soon disappears. First, let us say that to produce a 1:1 ratio of skipjack tuna larvae to all other tuna larvae, there should be 4 times as many skipjack tuna as all other tunas, since the fecundity of the skipjack tuna is roughly one-fourth that of other tunas (comparison made on the median number of eggs for skipjack tuna and for yellowfin and bigeye tunas). To produce a 2:1 ratio of larvae there should be 8 times more skipjack tuna as all other tunas. But since it requires roughly eight skipjack tuna to equal the average weight of all other tunas (taking 4.5 kg as the average weight of the skipjack tuna and 35.5 kg as the average weight of other tunas), the conversion factor for skipjack tuna yield to that of other tunas approaches a 1:1 ratio, far different from the 2:1 ratio used by Suda.

Other factors, either not considered or assumed to be equal for all tuna species in the above estimates are the mortality rates of eggs, larvae, and juveniles of the different species and the capability and efficiency of the various fishing gear used. Corrections for these factors could change the estimates further. Estimates 3, 4, and 5, based on yields proportional to that estimated for the Pacific (2), relative to the areas occupied by the skipjack tuna (or larvae) in the respective oceans, are equally speculative.

Despite the weaknesses in the various estimates of potential yield, sizable increases are still possible in most existing fisheries. The increases could come from harvesting more of the fish that escape capture within the fishing area by improving the gear or by following the fish further along the escape route, as noted by Rothschild (1966). This is especially applicable to the eastern Pacific fishery. In the western Pacific Ocean the situation is different. The escapement stocks from the Japanese coastal fishery, which include skipjack tuna of two subpopulations, are already being fished in the Japanese southern water fishery. The reduction in the catch rates noticed in the latter fishery (Kasahara, 1971), especially in the western sector or original fishing grounds, indicate that exploitation of skipjack tuna of the western Pacific subpopulation is nearing the maximum sustainable level. The increases in the western Pacific Ocean, therefore, must come from fish of the central-eastern Pacific subpopulation in the eastern sector of the Japanese southern water and coastal fisheries.

Sizable increases in yield should also be possible in several areas outside the present commercial fisheries. The locations of skipjack tuna stocks (Fig. 4), and the plots of catch rates of skipjack tuna taken on the tuna longline in 1969-71 (Fig. 5) should be useful in pointing out areas that could develop into new fishing grounds. In the Pacific Ocean most of such areas are in the southern hemisphere: the Marquesas-Tuamotu-Society Islands, the Phoenix-Tokelau-Samoa Islands, and the Tonga-Fiji-New Hebrides-New Caledonia Islands. A recent attempt at fishing in Tahitian waters (Society Islands) by a pole-and-line boat from Hawaii resulted in a catch of 182 tons of skipjack tuna in a 3-month period (January-March 1973). The catch compared favorably with that taken in the Hawaiian fishery during the peak months of the season (June-August). Commercial operations by the Japanese pole-and-line vessels in the waters of Papua-New Guinea, the Solomon Islands, and New Caledonia-New Hebrides Islands also have produced favorable results.

Worthy of investigation is the Leeward Islands area extending northwestward from the Hawaiian Islands to Midway. There are ample reports of tuna school sightings, based on a number of exploratory fishing cruises, to indicate possible concentrations of skipjack tuna there (Rothschild and Uchida, 1968). Farther to the northwest of the Leeward Islands, Japanese bait boats ventured to the Milwaukee Bank area (lat.31°-36°N, long.170°-174°E) in the summer (July-September) of 1972. Although the catches were small, the landings per boat-trip averaged 109 tons, much better than the average landings (71.9 tons) of boats fishing in the Japanese southern water fishery.

Skipjack tuna have not been taken as consistently in the Atlantic Ocean as in other oceans with the longline gear, and therefore other means must be used to locate possible areas of skipjack tuna abundance. On the basis of similarities in the westward flow of equatorial currents and their deflections to the north and south at the western extremities of the Atlantic and Pacific Oceans, it is reasonable to assume that skipjack tuna would be similarly distributed in both oceans. If so, areas favorable for skipjack tuna concentrations in the Atlantic Ocean should be off the southeastern coast of Brazil and from off the northeastern coast of Brazil through the West Indies. The eastern Atlantic area off the coast of Senegal to Angola is already developing into a fishery of major importance.

In the Indian Ocean the likely sources of skipjack tuna should be in the northwestern part from Madagascar to the Arabian Sea, and around the southern part of India beyond the

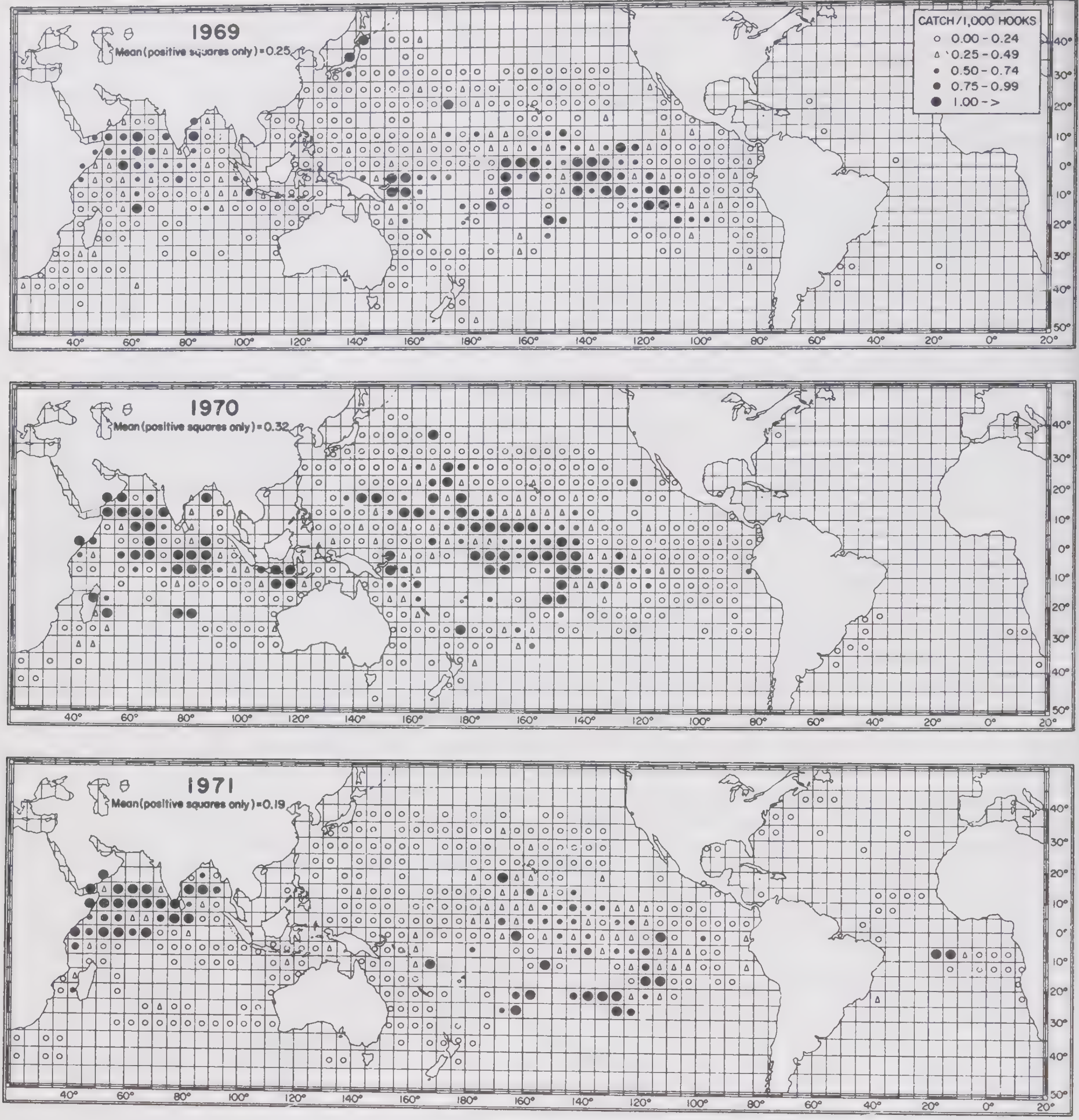
1969
Mean (positive squares only) = 0.25
CATCH / 1,000 HOOKS
○ 0.00 - 0.24
△ 0.25 - 0.49
• 0.50 - 0.74
● 0.75 - 0.99
● 1.00 ->
1970
Mean (positive squares only) = 0.32
1971
Mean (positive squares only) = 0.19
40° 60° 80° 100° 120° 140° 160° 180° 160° 140° 120° 100° 80° 60° 40° 20° 0° 20°
40° 30° 20° 10° 0° 10° 20° 30° 40° 50°

Figure 5.—Catch rates of skipjack tuna taken in the Japanese tuna longline fishery, 1969-71 (Fisheries Agency of Japan, 1971, 1972, 1973).

limits of the present drift-net fishery. Other possible areas are in waters off Sumatra and Java.

HARVESTING

The bulk of the skipjack tuna catches in the major oceans are made either by pole-and-line gear using live bait as chum or by purse seine. Both types of gear are used in the eastern Pacific, the Japanese near-coastal, and the eastern Atlantic fisheries. In the Japanese southern water fishery in the Pacific, however, the pole-and-line gear accounts for virtually the entire commercial catch of skipjack tuna.

There are advantages and disadvantages to either type of fishing. In pole-and-line fishing, the biggest problem is its dependence upon live bait. Not only must the bait be available, but the suitability and hardiness of the baitfish and the capability of keeping them alive over long periods must be adequate. Because of these problems, fishing by this method was for years limited to coastal waters. In recent years the Japanese have expanded their pole-and-line fishery into waters of the United States Trust Territory of the Pacific Islands by transporting baitfish from Japan. Because of the long distances to the fishing grounds and the need for large bait holding apacities, only large vessels (> 100 ons) were involved. At the present age of capability in bait handling and ait holding techniques, these vessels ave about reached the limit of their operational distance. Further expansion into the southern hemisphere or p to and beyond the international ate line in the northern hemisphere as to resort to the use of baitfish aken within the fishing area. However, most small Pacific islands lack suitable baitfish in sufficient quantities to upport any sizable fleet of large fishing vessels. An additional problem involved in this type of fishing is the response of skipjack tuna to the bait. Not all of the schools sighted are fished and not all of the schools fished result in catches. In the Hawaiian skipjack tuna fishery, for example, about 50 percent of the schools fished (chummed) do not result in catches (Rothschild and Uchida, 1968). There are advantages, however, to this type of fishing: (1) it can be done from small vessels, (2) any size school may be fished, and (3) it is not hampered by oceanographic conditions such as clear water and thermocline depth, nor by fast moving schools.

In purse seine fishing, problems associated directly with baitfish are eliminated, but other problems such as deep thermocline, clear water, and size and mobility of schools, are encountered. The traditional purse seine fisheries for skipjack tuna have been successful because the fishing area was characterized either by murky waters, shallow thermocline, or the presence of a marked front between warm and cold currents. In equatorial waters, however, the waters are exceptionally clear and the thermocline is deep enough to permit fish schools to escape by diving beneath the net before it has been pursed. This is not to say that there are no suitable seining sites in the equatorial areas. There are areas with shallow thermocline, especially along the edge of the equatorial counter-current, but the skipjack tuna are not limited in their distribution to these areas alone. Recent developments in net design, such as using monofilament nylon netting to make it lighter and increasing the size of the net, have improved the efficiency of the gear, but more improvement is needed in gear modification and specialized techniques if we wish to harvest skipjack tuna in equatorial waters.

The difficulties and problems faced in fishing for skipjack tuna by both pole-and-line and purse seine methods in distant waters certainly will not be solved overnight. Yet from the evidence presented in the foregoing discussions, it is more than likely that skipjack tuna are available in sizable quantitites in many areas not now fished commercially. For the immediate future, at least until modifications to the purse seine for mid-oceanic use have been made and tested successfully, the development of techniques to transport live baitfish over great distances could be the surest way to take advantage of the resource in the central Pacific.

The Japanese southern fishery operation has shown that the anchovy, *Engraulis japonicus*, can be transported successfully for distances up to nearly 2,000 miles. Furthermore it has been reported that this baitfish can normally survive for about 5 weeks (Yabe, 1972). If the eastern Pacific northern anchovy, *E. mordax*, which are plentiful in waters off California, are as hardy as their western Pacific counterpart, they or some other suitable baitfish could be transported to Hawaii and to other South Pacific islands. And, if the transporting of such a bait can be done quickly and in large enough quantities (a study has now been initiated by the Honolulu Laboratory to ship baitfish from California to Hawaii in sufficient quantities to supply the Hawaiian skipjack tuna fishing fleet), it should be possible for large bait boats stationed in Hawaii to exploit the Leeward Islands area up to and even beyond Midway and waters to the west and south of the Hawaiian Islands, well beyond the present 30- to 50-mile range of the Hawaiian fishery.

OPPORTUNITIES FOR THE UNITED STATES

Two points are brought to focus from the foregoing discussions. First, although all the large tuna species have already reached or are fast approaching their maximum sustainable yield levels, the skipjack tuna shows no such signs, except in the western equatorial Pacific. This is true in spite of the fact that the skipjack tuna is today the biggest yield producer among the species of tunas favored for commercial uses. Second, there are vast areas in the Pacific and other oceans that have not been fished, except by local, small-scale subsistence-type fisheries. In some areas not even this type of fishing has been done. The opportunities for development of the skipjack tuna fisheries in the Pacific hold true also in the Indian and Atlantic Oceans.

That the successful development of the skipjack tuna resource will be beneficial to the U.S. economy in many ways cannot be doubted. It will be a source of additional high-quality raw material for U.S. packers and reduce our dependence on foreign sources; it will increase employment opportunities for U.S. vessels and fishermen now restricted by catch quotas; it will in turn increase economic activity in other industries related to fishing; and finally, it will expand the economic base of the Pacific Islands, thus making their people more self-reliant and self-sufficient.

Although the resource is there, it remains fair game to all nations with the capability, desire, and willingness to develop it. In the Pacific, Japan has already begun to shift her emphasis from longlining for tunas towards fishing for skipjack tuna, and has entered into joint venture operations to fish in the Papua-New Guinea and Solomon Islands area. Fishing has been going on there since 1970. Japanese vessels also have begun to expand their operations into waters northwest of Midway. Other nations that have been longlining for tunas, such as Korea and Taiwan, have also come to realize that their future in fishing is in the skipjack tuna. In Korea a training center is now turning out skipjack tuna fishermen and both Korea and Taiwan are beginning to build up a fleet of skipjack tuna fishing vessels. If the United States is to get a fair proportion of the skipjack tuna resource, much has to be done and done quickly.

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Occurrence of Young Billfishes in the Central Pacific Ocean

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ABSTRACT

Plankton and other net-caught samples collected on past cruises of the National Marine Fisheries Service, Honolulu Laboratory vessels in Hawaiian and central Pacific equatorial waters were examined for billfish larvae and juveniles. Of the 342 billfish young found in 4,279 net tows, 209 were blue marlin, *Makaira nigricans*, 82 were shortbill spearfish, *Tetrapturus angustirostris*, 2 were sailfish, *Istiophorus platypterus*, 20 were swordfish, *Xiphias gladius*. Twenty-nine larvae were unidentified owing to excessive damage. A preponderance of the catches was obtained from hauls made at the surface during daylight.

In the equatorial central and North Pacific larvae of only three of the six billfish species nominally found in the Pacific were taken. The captures of these larvae (blue marlin, shortbill spearfish, and swordfish) fill the gaps in the known distribution of istiophorids and swordfish, and extend their distribution eastward to the Hawaiian Islands in the North Pacific. The two sailfish larvae were taken in New Hebrides waters in the western South Pacific.

The absence of striped marlin, *Tetrapturus audax*, larvae in Hawaiian waters was significant, since this species comprises nearly 82% of all istiophorids taken on the longline in the Hawaiian fishery. Their absence suggested that the striped marlin in Hawaiian waters probably migrate elsewhere to spawn. If this is true, then the spawning habits of this species differ significantly from those of blue marlin. A similar situation could hold for sailfish also.

In recent years fishery workers have given more attention to the early life history of billfishes, owing to the increasing importance of these fishes in the commercial and sport fishing catches. The billfishes in the Pacific Ocean are represented by two families: Istiophoridae and Xiphiidae. The Istiophoridae includes five species: *Istiophorus platypterus,* sailfish; *Tetrapturus angustirostris,* shortbill spearfish; *T. audax,* striped marlin; *Makaira nigricans,* blue marlin; and *M. indica,* black marlin. The Xiphiidae is represented by a single species, *Xiphias gladius,* swordfish. Larvae of all these species, mainly from the western Pacific, have been identified and reported by Japanese workers.

This study, based on larvae collected on past cruises of the National Marine Fisheries Service, Honolulu Laboratory (HL) vessels in Hawaiian and central Pacific equatorial waters, verifies the identifications reported by Yabe (1953), Yabe et al. (1959), Ueyanagi and Yabe (1959), and Ueyanagi (1959, 1962, 1964), and extends the distribution of larvae of certain billfishes eastward through the central Pacific.

IDENTIFICATION OF LARVAE

The three species of istiophorid larvae in our collection, blue marlin, sailfish, and shortbill spearfish, were easily identified on the basis of black pigmentation (Ueyanagi, 1963) on more than half the length of the lower jaw (sailfish) and on the branchiostegal membranes (shortbill spearfish). Larvae of blue marlin lacked this pigmentation. Since larvae of striped marlin also lack this pigmentation, the separation of blue from striped marlin is most difficult. Ueyanagi (1963) lists two main characters by which he separates the larvae of these two species: (1) the tip of snout either level or below center of eye (striped marlin), and (2) the "anterior edge of orbit projects forward" (blue marlin). The first character is highly subjective and lacks a clear definition of reference points. Even a slight distortion in the body can effect a change in the position of the eye relative to that of the tip of snout. The second

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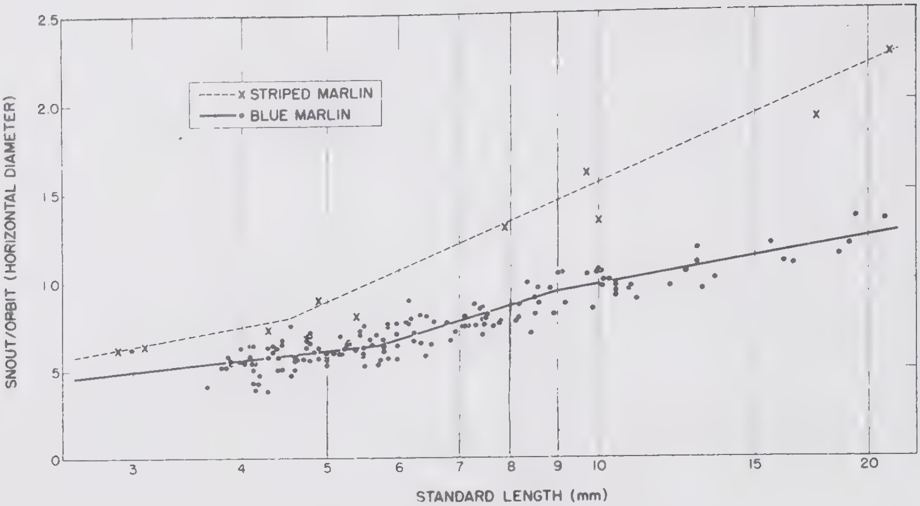

Figure 1.—Snout to orbit (horizontal diameter) ratios of blue and striped marlins. Growth stanzas fitted by Bartlett's best-fit line.

character needs clarification: it is the shape of the orbital crest as well as the extent of protrusion that sets the blue marlin larvae apart from those of striped marlin. In the blue marlin the anterior part of the orbital crest, beginning slightly ahead of the anterior naris, rises sharply and the anteriodorsal part is high and angular. In other istiophorid larvae the orbital crest slopes up and back more gradually (Ueyanagi, 1963, Plate 3).

A more useful character by which larvae of these two species can be separated is the snout to orbit ratio. Ueyanagi (1959) has used this character to show the difference between larvae of sailfish and blue marlin, except that his snout measurement included the distance from the tip of snout to center of eye with the orbit measured vertically. We have used snout length as measured from the tip to the anterior edge of the orbit and the orbit as measured horizontally. Regardless of which snout length or orbit measurement is used, the separation of the curves is similar.

Figure 1 shows the snout to orbit ratios of 138 blue marlin larvae from the central Pacific and 10 striped marlin from the western Pacific (seven measurements from Ueyanagi, 1964 and three measurements from specimens sent to us by Ueyanagi) plotted against standard length. Bartlett's (1949) best-fit lines were drawn through points representing growth stanzas for each species. Despite the small number of points shown for striped marlin, the separation of the species, at least in the larger size range, appears to be valid. Among the smaller stages (below 6 mm), however, the points approach each other close enough to make separation more difficult.

The scatter of points about the curve shown for blue marlin above 6 mm (Fig. 1) and the absence of snout to orbit ratios falling near the curve shown for striped marlin suggest that larvae from the central North Pacific without pigmentation on the posterior half of the lower jaw and branchiostegal membranes are all of blue marlin.

COLLECTION OF SAMPLES AND CATCHES

The samples of billfish larvae were obtained mainly from 1-m plankton net tows taken from vessels of the HL and other organizations from 1950 through 1970, and from 1- × 2-m neuston net tows in 1971. The plankton net was usually towed for 30 min, either horizontally at the surface or obliquely to depths ranging from 40 to 200 m. The neuston net, constructed entirely of 1-mm mesh netting, was used only on one cruise to the western Pacific. Owing to operational difficulties, this net was towed at the regular plankton net speed of 3.7-5.5 km/h for 30 min. Catches by the plankton and neuston nets included juveniles as large as 20 mm. A 12.2-m mouth diameter Cobb pelagic trawl, made of 19.0-mm stretch mesh netting lined with 6.4-mm netting at the cod end, was used on several cruises around Hawaii, in equatorial waters along long. 145°W, and in waters of the Trust Territory of the Pacific Islands from 1967 through 1971, and caught juveniles as large as 55 mm. The midwater trawl was usually towed at night for 3-6 h (Appendix Table 1). The area sampled with towed nets is extensive, covering nearly one-half of the Pacific Ocean (Fig. 2).

A total of 342 billfish larvae and juveniles was obtained from 4,279 net tows of all types. A summary of the catch by type of gear and tow (Table 1) shows that 4,170 tows (97%) were made with the 1-m plankton net, and that of this number 2,850 (68%) were oblique tows. Despite the large ratio of oblique to surface tows (2:1), the catch ratio was just the opposite. The surface tows caught five times as many larvae and juveniles as the oblique tows.

A closer look at the 1-m net tows by depth and time of day (Table 2) shows that most of the larvae were taken in the upper 1-m of water during daylight. The small numbers taken in the oblique tows suggest that these larvae are restricted to the surface, and the small catches in night tows suggest that these larvae migrate downward at night. Both observations are similar to the results obtained by Ueyanagi (1964) in the western Pacific, where he examined 32 day and 31 night plankton net samples from depths of 0, 20, and 40 m. He found that abundance of larvae decreased with depth during the day, and that the day catches at the surface were greater than those at night. His data point out one other aspect which does not appear in our data: that within the upper 40 m of

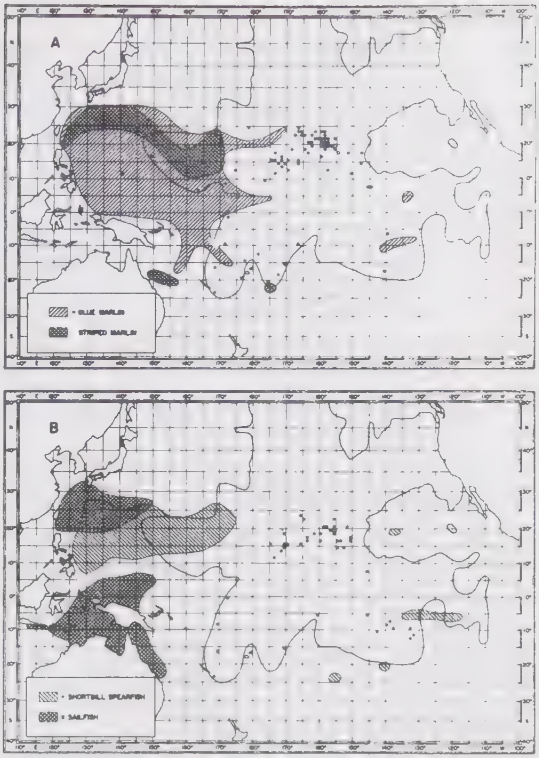

Figure 2.—Localities of captures of young Istiophoridae in the Pacific Ocean. Area sampled by the Honolulu Laboratory indicated by solid line and capture sites by black dots. Localities of captures by Howard and Ueyanagi (1965) shown as shaded areas.

Table 1.—Billfish larvae and juveniles collected by various gear from research vessels of the Southwest Fisheries Center, Honolulu Laboratory in the central Pacific Ocean, 1950-71.

			Larvae and juvenile catch						
Gear	Type of tow	Number tows	Blue marlin	Shortbill spearfish	Sailfish	Swordfish	Damaged unidentified	Total	Percent
1-m plankton net	30-min, surface	1,320	142	68	2	16	22	250	73.1
1-m plankton net	30-min, 40-200m oblique	2,850	25	14	0	4	7	50	14.6
Cobb pelagic trawl	6-h, 20-100m horizontal	92	18	0	0	0	0	18	5.3
1 × 2 m neuston net	30-min, surface	17	24	0	0	0	0	24	7.0
Totals		4,279	209	82	2	20	29	342	100.0
Percent			61.1	24.0	0.6	5.8	8.5	100.0	

Table 2.—Catch rates (catch per 100 tows) of billfish larvae in 1-m plankton net and 1- × 2-m neuston net.

			Species									
	No. of tows		Blue marlin		Short-bill spearfish		Sailfish		Swordfish		All species including unidentified larvae	
Type of tow	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Surface	201	1,119	50.0	3.7	14.8	3.5	1.0	0.0	2.0	1.1	74.2	8.9
Oblique	1,280	1,570	0.7	1.0	0.4	0.5	0.0	0.0	0.2	0.1	1.5	2.1
Neuston	15	0	160.0	—	0.0	—	0.0	—	0.0	—	160.0	—

water, the catches at night at the three depths sampled were approximately equal.

The neuston net catches (Table 2) provide further information on the vertical distribution of these larvae. The net was normally towed with part of the net above the surface, so that on an average it only sampled the upper 0.5 m of water. The catch per tow was more than three times that of the 1-m net towed fully submerged at the surface. Since the neuston net strained roughly twice the volume of water as the 1-m net, the catch per unit volume of water strained was about 1.5 times that of the 1-m net. The higher catch rate of the neuston net thus suggests that billfish larvae could be concentrated not only in the upper 1-m of water but even closer to the surface.

DISTRIBUTION OF ISTIOPHORID LARVAE

Howard and Ueyanagi (1965) have plotted the occurrence of istiophorid larvae in the Pacific Ocean. Outlines drawn of their plots by species (Fig. 2) show that catches of most species were largely confined to the western Pacific. Our data of larval captures fill the gaps in the distribution given by Howard and Ueyanagi (1965), particularly around the Hawaiian Islands and in the central Pacific south of the equator. The northern limits of distribution of the four species of Istiophoridae in the western North Pacific are notably similar (Fig. 2, panels A and B). The southern limits of distribution for all species cannot be defined, since sampling for the larvae on all cruises east of long. 180° did not extend far enough southward. Judging on the basis of the close relationship between larval distribution and the 24°C surface isotherm (Ueyanagi, 1964; Jones and Kumaran, 1964) and on the configuration of the surface temperature isotherms across the South Pacific (U.S. Hydrographic Office, 1948), it seems that the southern limits of distribution of these larvae should not extend much beyond lat. 25°S.

Blue Marlin

Blue marlin larvae, which comprised 60.8% of all billfish larvae collected by us, occurred in both the North and South Pacific. In the North Pacific they were distributed heavily around the Hawaiian Islands and in waters to the west between lat. 7° and 24°N. This distribution seems to be contiguous with that shown by Howard and Ueyanagi (1965). In the South Pacific the larvae occurred in a band between lat. 0° and 24°S from the New Hebrides through the Tuamotu Archipelago. The western end of this band ties in with the southwestern outline of the distribution of Howard and Ueyanagi (1965). The intervening area (lat. 5°-10°N and long. 140°W-180°) appears to be devoid of blue marlin larvae, but this could be due to inadequate sampling; only a few surface day tows were made there. Sampling especially for billfish larvae would likely change this distributional picture and provide us with better information in the area east of long. 140°W and in equatorial waters westward to long. 180°.

Seasonal Distribution.—Seasonal changes in the distribution of blue marlin larvae were observed only in the Hawaiian Islands area, where enough seasonal sampling was done (Fig. 3). The blue marlin, as well as some other billfishes, spawn throughout the year in warm tropical and subtropical waters. At both the northern and southern fringes of distribution, however, spawning occurs only during the warm seasons (Howard and Ueyanagi, 1965). In the Hawaiian Islands area, the northern fringe of larval blue marlin distribution lies roughly parallel to the surface isotherms (Fig. 3) and moves northeastward and southwestward with the seasons. Thus, in the first quarter the larvae were found far south of the island, but in the second quarter they were abreast of the islands. In the third quarter the edge of larval distribution shifted northward a few degrees of latitude past the islands and moved back to just south of the islands in the fourth quarter. The northward shift of the distribution during the four seasons is about 10° to 11° of latitude.

Ueyanagi (1964) reports that larvae of istiophorid species occur generally in water that is warmer than 24°C. Jones and Kumaran (1964) also show that none of their larvae were taken in waters colder than 24.5°C. Our data (Appendix Table 1) show that although most of the blue marlin larvae were taken in water between 26° and 29°C, the lowest temperature associated with capture was 23.8°C.

Shortbill Spearfish

Larvae of shortbill spearfish comprised 24.3% of all billfish larvae collected by us. Their distributional pattern in the central Pacific is similar to that of blue marlin larvae (Fig. 2). North of the equator the captures were grouped around the Hawaiian Islands in an area bounded by lat. 10° and 23°N and long. 150° and 174°W. The area between long. 174°W and the eastern limit of Howard and Ueyanagi's (1965) data should also contain larvae of this species to show a continuous distribution from the western Pacific to the Hawaiian Islands. Because of inadequate sampling, only three surface day tows and eight oblique tows, no larvae were taken there.

South of the equator, larvae were taken in a band (lat. 0° to approximately 20°S) extending from the New Hebrides Islands through the Tuamotu Archipelago, similar to that for blue marlin. The gap in the distribution along the equator, between lat. 7°N and 5°S, may be interpreted in two ways: first, the gap could be due to insufficient samples of surface day tows; and second, the gap could represent a separation of the shortbill spearfish into northern and southern populations. The latter is supported

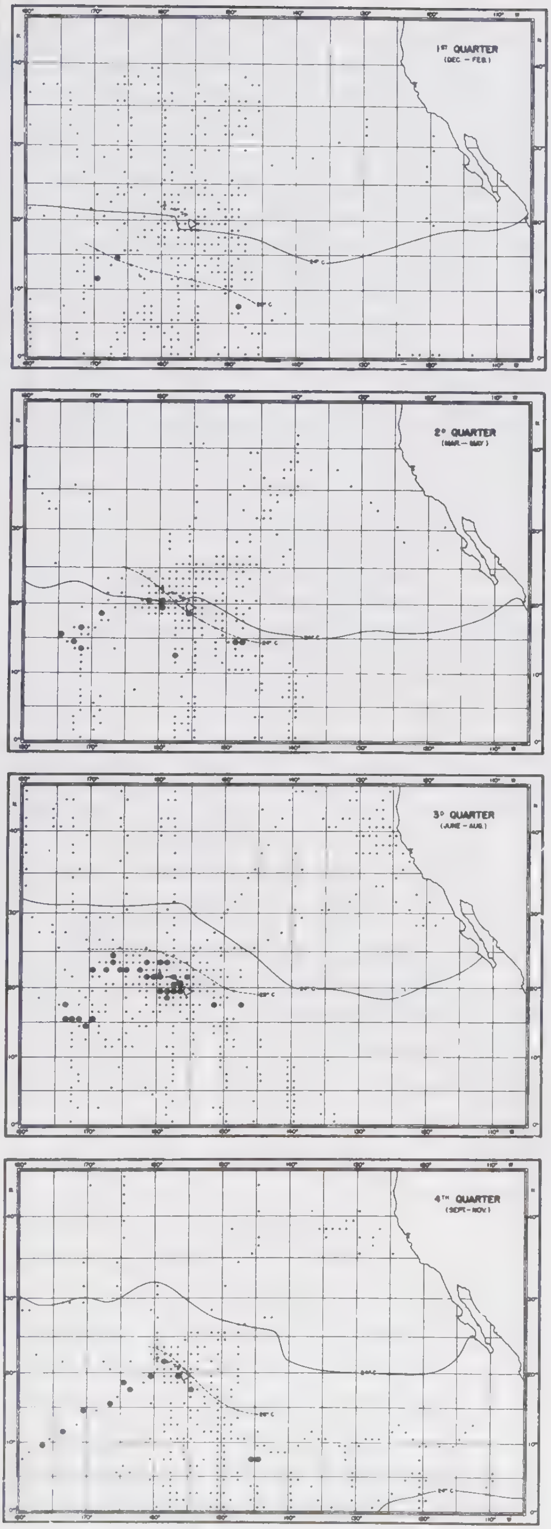

Figure 3.—Localities of captures of young blue marlin by quarters. Solid lines represent mean surface temperature for last month of quarter. Dashed lines represent surface temperature at time of sampling. Small open circles represent sampling with plankton nets in 1° square area; large solid dots represent capture sites.

by the discontinuous north-south distribution of larvae in the western Pacific, compared with the continuous distribution across the equator of blue marlin larvae.

Seasonal Distribution.—The seasonal occurrence of shortbill spearfish larvae in the Hawaiian Islands (Fig. 4) resembles that of blue marlin in certain respects, the northern edge of distribution being parallel to the chain of islands and the movement across the islands being from southwest to northeast. The differences, though small, are nevertheless evident. In the first quarter shortbill spearfish larvae were found approximately 500 km southwest of the islands, as compared to about 950 km for blue marlin larvae. The northern edge of the larval distribution shifted northeastward to about 320 km past the islands in the second quarter, retreated to the islands in the third quarter, and continued southwestward past the islands in the fourth quarter. This north-south movement of larval shortbill spearfish distribution seemed to precede that of larval blue marlin distribution by a full quarter.

One reason for these differences could be that the shortbill spearfish may be able to spawn in colder water than the blue marlin. The temperature data seem to suggest this. Shortbill spearfish larvae were found in waters with temperatures as low as 22.3°C, with most catches having been made in 25° to 26°C water. Both minimum and best catch temperatures for shortbill spearfish larvae were at least 1°C lower than for blue marlin larvae.

DISTRIBUTION OF XIPHIID LARVAE

Larvae of the Xiphiidae, the second of two families that make up the billfishes, were taken only occasionally. Only 20 specimens ranging in sizes from 5.8 to 23.0 mm were found in plankton samples taken from 1950 through 1971 (Table 1 and Appendix Table 2).

Larval and juvenile stages of swordfish from the Atlantic and Pacific Oceans have been described by a number of workers (Arata, 1954; Nakamura et al.,

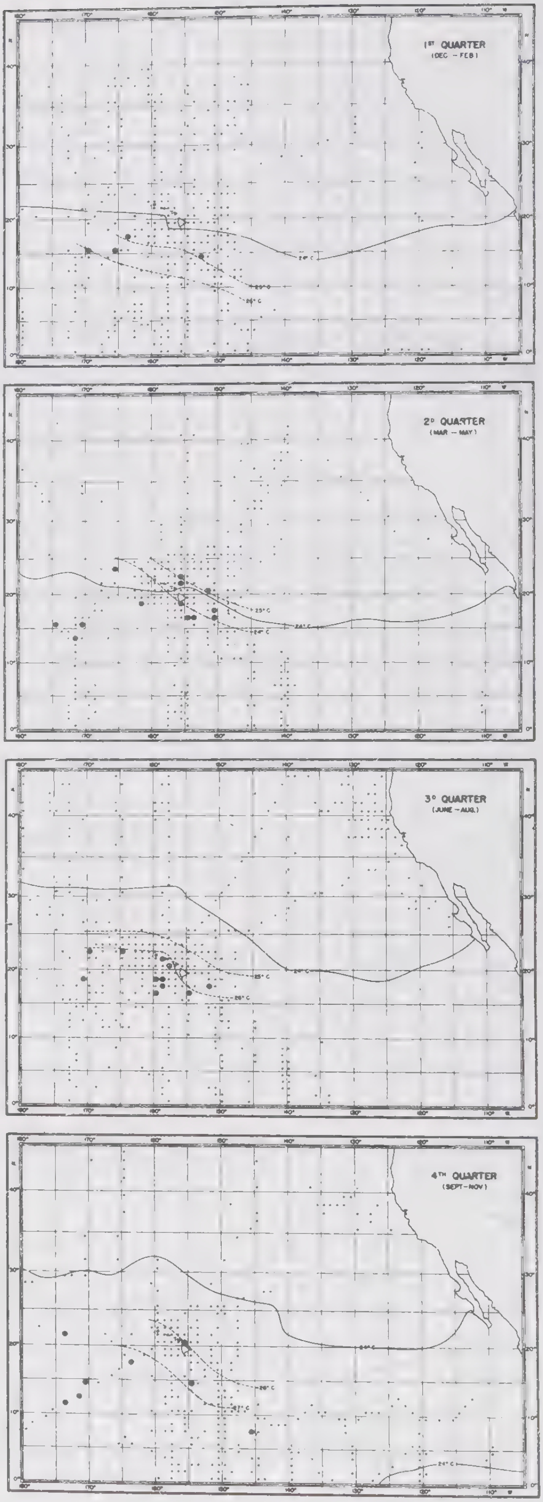

Figure 4.—Localities of captures of young shortbill spearfish by quarters. Solid lines represent mean surface temperature for last month of quarter. Dashed lines represent surface temperature at time of sampling. Small dots represent sampling with plankton nets in 1° square area; large dots represent capture sites.

1954; Yabe, 1951; and Yabe et al., 1959). The swordfish larvae are easily recognized by their long snouts and heavily pigmented elongate bodies. They have a prominent supraorbital crest similar to that of the marlins, but lack the enlarged posttemporal and preopercular spines. Larvae above 8.0 mm are even more distinctive; they have one or more rows of spinous scales on each side of the dorsal and anal fins, with those along the latter continuing forward to the level of the pectoral fin.

Although the important fishing areas for this species are mainly in temperate waters, the larvae and juveniles are found largely in tropical and subtropical waters throughout most of the Pacific. Figure 5 shows the locations of captures of swordfish larvae and juveniles below 80.0 mm recorded to date and those taken by HL ships. A similar plot of captures, exclusive of those taken by HL, was published by Jones and Kumaran (1964). (One capture site at lat. 23°N, long. 174°W is plotted erroneously. This should have been in the southern hemisphere.) Our samples extend the distribution of young swordfish to waters east of the Hawaiian Islands in the North Pacific, and partially fill in the gap between long. 132° and 172°W in the equatorial and South Pacific. The overall distribution, which extends roughly two-thirds the breadth of the Pacific, is similar to that of blue marlin larvae.

Although captures were spotty throughout the western and central Pacific, there were enough to show differences in spawning time in the various parts of the Pacific. The probable month of spawning (Fig. 5) was calculated for each individual, using the growth estimate of 0.6 mm per day derived by Arata (1954). According to these calculations spawning occurred in spring and summer (March through July) in the central North Pacific and in spring (September through December) in the western South Pacific south of lat. 10°S. In equatorial waters between lat. 10°N and 10°S, spawning occurred in all months of the year. Spawning also seemed to begin and end 1 or 2 mo earlier in the western Pacific in the Philippine-Formosa area, as compared with the Hawaiian Islands area. This is understandable when we consider: (1) that post-larval swordfish are usually taken in the Atlantic in waters having surface temperatures above 23.5°C (Taning, 1955), (2) that in the western Pacific this isotherm lies between Taiwan and the Philippine Islands as early as February, and (3) that in the central Pacific along the same latitude, the 23.5°C isotherm passes northward through the Hawaiian Islands in March or April, a difference of 1 to 2 mo.

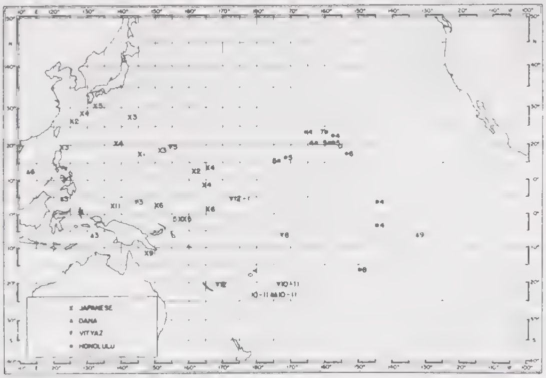

Figure 5.—Localities of captures of young swordfish <80 mm SL in the Pacific. (The numerals next to each capture site denote estimated month of spawning.)

Table 3.—Summary of young swordfish *(Xiphias gladius)* taken in plankton net tows in the Atlantic and Pacific Oceans.

Source[1]	No. of larvae <10 mm	No. of juveniles 10-80 mm	Total
Yabe (1951)	0	1	1
Arata (1954)	4	19	23
Yabe et al. (1959)	5	15	20
Sun Tsi-Gen (1960)	0	17	17
Honolulu Laboratory	14	6	20
Total	23	58	81
Percent	28.4	71.6	100

[1] Tåning (1955) examined 60 larvae of which 53 were <20 mm; no breakdown of larvae <10 mm available.

A unique aspect about the captures of swordfish young is that of the small numbers taken in plankton nets, only 28.4% were larvae smaller than 10 mm (Table 3). Among other pelagic fishes, such as spearfishes, tunas, mackerels, etc., most of the larvae caught in plankton nets are below 10 mm. Perhaps the proportion of larvae caught is reduced inordinately by the disproportionate catches of juveniles. Among other fishes, particularly tunas and mackerels, juveniles above 10 mm are rarely caught, except in much larger gear such as midwater trawls. The large percentage of juveniles up to 80-mm long taken in plankton nets suggests that the swordfish young either do not react to the net quickly enough to avoid it or are exceptionally poor swimmers at this stage of development.

Also noteworthy is the apparent brevity of the spawning season in the northern and southern edges of distribution. Although spawning is indicated for most months of the year in the vicinity of the equator, it extended for only 4 mo, April to July, in the areas above lat. 20°N. By contrast, blue marlin and shortbill spearfish spawning extended over 5 and 6 mo, May through September and May through October, respectively, in Hawaiian waters.

The captures of swordfish larvae off Hawaii also provided new information on the lowest temperatures in which this species spawn. Two larvae (9.6 and 9.8 mm) were taken at long. 157°W in 23.3° and 23.6°C water, well below the lowest temperature previously recorded in the Pacific and comparable to the 23.5°C recorded from the southwestern Atlantic by Tåning (1955).

DISCUSSION

A comparison of the species composition of billfishes taken on the longline and the young taken in plankton nets in Hawaiian waters leads to interesting speculations concerning the spawning behavior of certain istiophorids. For example, the striped marlin is the predominant species taken commercially, in terms of both number and weight of fish caught. An average of 5,685 striped marlin, which make up 81.6% of all istiophorids caught on the longline, were taken annually from 1966 to 1970. Yet, no larva of this species has been recognized from our samples. Alternatively, blue marlin and shortbill spearfish comprise only 9.8% and 3.4%, respectively, of the istiophorids taken on the longline, but they make up the entire catch of young taken in these waters. Larvae of sailfish and black marlin also have not been recognized in our catches. These two species combined represent only 4.5% of the istiophorids taken on the longline.

The absence of striped marlin larvae in Hawaiian waters is probably due to absence of spawners. Length-frequency data (Royce, 1957; Howard and Ueyanagi, 1965) show that very young fish less than 150-cm modal length (11 kg[2]) first appear in the fishery in the fall and remain there continuously through two successive seasons, by which time they have attained a modal length of 220 cm (45 kg). No one has yet studied the size of striped marlin at initial spawning but it is suspected that fish in the last modal group may have reached sexual maturity, since fish of similar sizes were found with ripe gonads in the western Pacific between lat. 15° and 30°N (Howard and Ueyanagi, 1965). A more striking phenomenon about the striped marlin fishery in Hawaii is that fish in the last modal group disappear in July and do not reappear as a group in the fishery. To be sure striped marlin larger than this modal size have been taken there but only in small quantities comprising less than 1% of the total monthly catches.

On the basis of the discussion above and the occurrence of both larvae and adults with ripe gonads only in the area between lat. 15° and 30°N, west of long. 170°E (Howard and Ueyanagi, 1965) in the North Pacific, it is logical to assume that the striped marlin in Hawaiian waters leave the islands to spawn, most likely in the western North Pacific. If this is so, the spawning habit of this species differs significantly from that of blue marlin, which spawn almost continuously between lat. 30°N and 25°S in the western and central Pacific.

The absence of sailfish larvae in the central Pacific, except in the western South Pacific (New Hebrides Islands), suggests that this species also may spawn in selective areas.

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[2] Conversion of weight (lb) to estimated length (cm) through courtesy of R.A. Skillman, Honolulu Laboratory.

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Appendix Table 1.--Record of catches of istiophorid larvae and juveniles by the Southwest Fisheries Center, Honolulu Laboratory from 1950 to 1971.

Gear	Type of tow	Depth of tow	Vessel[1]/ cruise/ station sample	Date	Time	Position		Duration of tow		Volume of water strained	Surface temperature	Surface salinity	Larval and juvenile catches[2]						Size range
						Latitude	Longitude	Hr.	Min.	m^3	° C	°/°°	SF	BL	SB	BB	UN	Total	mm
1-m plankton net	Horizontal	0	S-4-24-1	5/14/50	0820	22°45' N	155°49' W	-	-	1255	22.9	-	-	-	1	-	-	1	5.0
Do.	do.	0	S-4-23-1	5/14/50	1852	22°40' N	157°10' W	-	-	2192	23.3	-	-	-	-	1	-	1	ca. 9.6
Do.	do.	0	S-4-4-1	5/17/50	1640	20°14' N	161°08' W	-	-	2125	24.2	-	-	1	-	-	-	1	4.5
Do.	do.	0	S-4-6-1	5/18/50	1048	19°25' N	159°50' W	-	-	2272	24.8	-	-	1	-	-	-	1	4.3
Do.	do.	0	S-4-7-1	5/18/50	1835	20°14' N	159°50' W	-	-	2967	24.9	-	-	1	-	-	-	1	5.0
Do.	do.	0	S-4-15-1	5/21/50	1610	20°13' N	158°30' W	-	-	2950	24.5	-	-	-	-	2	-	2	10.5, ca. 19.3
Do.	do.	0	S-4-20-1	5/23/50	0911	20°14' N	157°04' W	-	-	3346	23.6	-	-	-	-	1	-	1	6.6
Do.	do.	0	S-4-25-1	5/24/50	1333	21°54' N	155°48' W	-	-	2645	22.3	-	-	-	1	-	-	1	4.5
Do.	do.	0	S-4-28-1	5/25/50	1740	18°34' N	155°48' W	-	-	3169	23.8	-	-	1	-	-	-	1	4.6
Do.	do.	0	S-6-14-1	8/18/50	1720	20°50' N	158°32' W	-	-	2287	-	-	-	3	-	-	1	4	3.9-7.1
Do.	do.	0	S-6-16-1	8/19/50	0750	19°24' N	158°23' W	-	-	3380	26.6	-	-	4	-	-	-	4	4.3-5.3
Do.	do.	0	S-6-17-1	8/19/50	1522	18°30' N	158°29' W	-	-	2240	26.7	-	-	2	1	-	-	3	3.7-3.8
Do.	do.	0	S-6-18-1	8/20/50	0210	18°32' N	157°08' W	-	-	1609	26.2	-	-	-	-	-	1	1	3.4
Do.	do.	0	S-6-19-1	8/20/50	2311	19°31' N	157°10' W	-	-	2728	26.0	-	-	-	-	-	1	1	5.5
Do.	do.	0	S-6-20-1	8/21/50	0815	20°23; N	157°07' W	-	-	2112	26.2	-	-	1	2	-	-	3	3.1-5.2
Do.	do.	0	S-6-21-1	8/21/50	1412	20°56' N	157°10' W	-	-	2767	25.8	-	-	1	-	-	-	1	2.8
Do.	do.	0	S-6-25-1	8/22/50	1500	21°56' N	155°45' W	-	-	2816	25.7	-	-	4	-	-	-	4	4.0-6.0
Do.	do.	0	S-6-22-1	8/23/50	1754	21° 50' N	157°10' W	-	-	2586	25.7	-	-	1	-	-	-	1	6.0
Do.	do.	0	S-6-12-1	8/24/50	1250	22°43' N	158°26' W	-	-	2106	-	-	-	2	-	-	-	2	5.2, 6.3
Do.	do.	0	S-6-11-1	8/25/50	0500	23°27' N	159°46' W	-	-	2374	-	-	-	2	-	-	-	2	5.1, 6.7
Do.	do.	0	S-6-1-1	8/25/50	1405	23°30' N	161°06' W	-	-	2047	26.0	-	-	2	-	-	-	2	5.1, 5.5
Do.	do.	0	S-6-3-1	8/26/50	1042	21°10' N	161°03' W	-	-	2150	26.7	-	-	2	-	-	-	2	4.5, 5.5
Do.	do.	0	S-6-4-1	8/26/50	1750	20°20' N	161°05' W	-	-	2251	26.7	-	-	-	-	-	4	4	4.6-5.6
Do.	do.	0	S-6-6-1	8/27/50	0950	19°26' N	159°50' W	-	-	2393	26.0	-	-	3	-	-	-	3	4.7-6.7
Do.	do.	0	S-6-9-1	8/28/50	1350	21°05' N	159°50' W	-	-	2456	26.0	-	-	3	-	-	-	3	5.4-10.2
1-m plankton net	horizontal	0	S-38-59-3	3/3/57	2035	17°48' S	135°06' W	-	-	1176		-	-	1	-	-	-	1	ca. 3.9
Do.	do.	0	S-38-62-3	3/17/57	2147	5°01' S	144°57' W	-	-	1778	28.7	35.37	-	-	1	-	-	1	3.3
Do.	do.	0	S-39-21-1	5/9/57	2010	23°03' N	165°23' W	-	-	-	25.1	35.21	-	-	6	5	-	11	SB 3.8-5.2, BB ca. 7.3-15.8
Do.	do.	0	S-39-28-1	5/15/57	2010	20°03' N	162°04' W	-	-	-	25.1	34.96	-	-	-	3	-	3	ca. 6.5-20.0
Do.	do.	0	G-30-14	8/23/56	0747	9°22' S	132°10' W	-	-	1670	25.2	35.41	-	-	1	-	-	1	6.5
Do.	do.	0	G-30-15-1	8/23/56	1954	9°48' S	132°07' W	-	-	1672	25.4	35.41	-	-	1	-	-	1	ca. 5.5
Do.	do.	0	G-30-17-4	8/24/56	2035	11°10' S	131°56' W	-	-	1776	25.0	35.71	-	-	1	-	-	1	4.2
Do.	do.	0	G-30-18	8/25/56	0750	12°12' S	132°05' W	-	-	1891	24.7	35.79	-	-	2	-	-	2	5.2, 6.0
Do.	do.	0	G-30-29-1	8/30/56	2000	9°22' S	137°01' W	-	-	1505	25.7	35.66	-	-	1	-	-	1	ca. 4.1
Do.	do.	0	G-30-31	9/1/56	0756	7°32' S	138°54' W	-	-	2021	25.6	35.64	-	-	7	-	-	7	ca. 5.2-7.2
Do.	do.	0	G-30-33	9/2/56	0750	8°50' S	139°08' W	-	-	1380	25.7	35.84	-	-	1	-	-	1	8.6
Do.	do.	0	G-45-29-2	7/29/59	1958	16°48' N	154°38' W	-	-	1284	25.9	-	-	-	1	-	-	1	ca. 4.3
Do.	do.	0	G-48-61	7/24/60	1955	16°04' N	160°08' E	-	-	-	28.9	-	-	1	-	-	-	1	5.1
Do.	do.	0	G-48-63	7/25/60	2000	18°16' N	160°11' E	-	-	-	28.9	-	-	2	-	-	1	3	4.0-4.5
Do.	do.	0	G-48-65	7/26/60	2000	19°56' N	160°09' E	-	-	-	28.8	-	-	2	-	-	-	2	4.3, 5.2
Do.	do.	0	G-53-17-1	7/8/61	1120	18°46' N	158°46' W	-	-	1675	26.0	34.68	-	-	1	-	-	1	7.6
Do.	do.	0	G-53-19-1	7/9/61	1107	16°01' N	159°55' W	-	-	2374	25.8	34.54	-	1	1	-	-	2	BL 6.0, SB 8.7
Do.	do.	0	G-53-27-1	7/12/61	1005	22°07' N	164°37' W	-	-	1803	26.2	35.05	-	-	1	-	-	1	10.1
Do.	do.	0	G-53-32-1	7/15/61	1000	22°58' N	169°21' W	-	-	2082	26.5	34.97	-	2	1	-	-	3	4.1-4.9
Do.	do.	0	G-53-34-1	7/16/61	1000	19°42' N	169°41' W	-	-	2097	26.9	34.84	-	-	-	-	1	1	8.0

Appendix Table 1.--Record of catches of istiophorid larvae and juveniles by the Southwest Fisheries Center, Honolulu Laboratory from 1950 to 1971.--Continued.

Gear	Type of tow	Depth of tow	Vessel[1]/ cruise/ station sample	Date	Time	Position		Duration of tow		Volume of water strained	Surface temperature	Surface salinity	Larval and juvenile catches[2]						Size range
						Latitude	Longitude						SF	BL	SB	BB	UN	Total	
								Hr.	Min.	m³	° C	°/..							mm
1-m plankton net	horizontal	0	G-53-42-1	7/22/61	1009	22°29' N	167°05' W	-	-	1980	26.5	35.00	-	1	-	-	-	1	17.2
Do.	do.	0	G-53-46-1	7/24/61	1103	22°33' N	162°04' W	-	-	1865	26.4	34.83	-	2	-	-	-	2	5.5, 12.6
Do.	do.	0	G-53-48-2	7/25/61	0207	20°25' N	162°15' W	-	-	1691	26.9	34.84	-	1	-	-	-	1	4.4
Do.	do.	0	G-53-49-1	7/25/61	1104	19°02' N	162°07' W	-	-	2061	27.0	34.73	-	1	-	-	-	1	9.0
Do.	do.	0	G-53-52-2	7/27/61	0209	18°57' N	159°59' W	-	-	2213	26.3	34.67	-	-	1	-	1	2	4.0-4.4
Do.	do.	0	G-53-54-2	7/27/61	2105	21°50' N	159°54' W	-	-	1851	26.5	-	-	-	-	-	1	1	4.9
Do.	do.	0	G-54-4-1	10/ 1 /61	2007	14°14' N	154°32' W	-	-	1770	26.9	34.42	-	-	1	-	-	1	6.0
Do.	do.	0	G-55-5-1	1/17/62	1000	17°00' N	163°00' W	-	-	-	25.0	-	-	-	1	-	-	1	4.3
Do.	do.	0	G-55-7-1	1/18/62	0558	15°06' N	165°15' W	-	-	-	25.0	-	-	-	3	-	-	3	4.5-6.4
Do.	do.	0	G-55-8-1	1/18/62	1713	14°03' N	166°39' W	-	-	-	26.0	-	-	1	-	-	-	1	6.2
Do.	do.	0	G-55-11-1	1/19/62	1544	12°05' N	169°01' W	-	-	-	26.8	-	-	2	-	-	-	2	8.9, 9.9
Do.	do.	0	G-55-12-2	1/19/62	1903	11°47' N	169°19' W	-	-	-	27.1	-	-	-	-	-	1	1	3.8
Do.	do.	0	G-55-26-2	1/29/62	1356	9°40' S	171°38' E	-	-	-	29.2	-	-	5	-	-	1	6	3.5-10.2
Do.	do.	0	G-55-34-2	2/1/62	0758	15°36' S	169°52' E	-	-	-	28.7	-	-	-	-	-	1	1	3.8
Do.	do.	0	G-55-35-2	2/1/62	1355	16°16' S	169°28' E	-	-	-	28.5	-	2	-	-	-	-	2	4.6, 4.7
Do.	do.	0	G-55-36-2	2/1/62	2015	16°40' S	168°57' E	-	-	-	28.5	-	-	2	-	-	-	2	3.8
Do.	do.	0	G-55-53-1	2/15/62	0805	19°37' S	176°43' E	-	-	-	27.2	-	-	9	-	-	1	10	4.0-6.5
Do.	do.	0	G-55-62-1	2/23/62	0810	14°59' S	177°13' E	-	-	-	28.7	-	-	2	-	-	1	3	3.8-5.3
Do.	do.	0	G-55-85-1	3/1/62	2100	18°48' S	176°31' W	-	-	-	28.6	-	-	-	-	-	1	1	4.3
Do.	do.	0	G-55-86-2	3/2/62	0809	20°21' S	175°42' W	-	-	-	27.7	-	-	1	-	-	-	1	10.4
Do.	do.	0	G-55-102-1	3/13/62	1957	15°05' S	170°48' W	-	-	-	28.3	-	-	2	1	-	-	3	4.3-4.5
Do.	do.	0	G-55-111-2	3/22/62	0803	9°52' S	166°16' W	-	-	-	28.8	--	-	1	-	-	-	1	4.0
Do.	do.	0	G-58-49	7/15/62	1342	23°27' N	164°51' W	-	-	2080	26.5	34.94	-	1	-	-	-	1	8.4
Do.	do.	0	G-58-53	7/16/62	0100	24°17' N	166°15' W	-	-	2427	25.6	35.06	-	3	-	-	-	3	3.8-4.7
Do.	do.	0	G-58-60	7/17/62	0100	22°55' N	165°41' W	-	-	1644	26.5	34.93	-	1	-	-	-	1	3.9
Do.	do.	0	G-58-63	7/17/62	1300	22°10' N	164°12' W	-	-	1212	26.5	34.98	-	1	-	-	-	1	10.3
Do.	do.	0	G-69-1-1	10/8/63	0827	19°44' N	160°15' W	-	-	-	27.1	-	-	1	-	-	-	1	ca. 13.9
Do.	do.	0	G-69-3-1	10/9/63	0755	17°39' N	163°33' W	-	-	-	27.2	-	-	1	2	-	-	3	BL 9.4, SB 4.2, 18
Do.	do.	0	G-69-5-1	10/10/63	0754	15°24' N	166°55' W	-	-	-	27.3	-	-	7	-	-	-	7	4.3-6.0
Do.	do.	0	G-69-7-1	10/11/63	0757	14°32' N	170°22' W	-	-	-	27.8	-	-	2	1	-	-	3	7.6-11.5
Do.	do.	0	G-69-9-1	10/12/63	0757	11°30' N	173°35' W	-	-	-	28.2	-	-	11	2	-	-	13	5.9-13.3
Do.	do.	0	G-69-11-1	10/13/63	0758	9°11' N	176°48' W	-	-	-	28.2	-	-	2	-	-	-	2	3.8, 4.3
Do.	do.	0	G-69-27-1	10/22/63	0156	0°53' S	172°18' W	-	-	-	-	-	-	-	1	-	-	1	3.4
Do.	do.	0	G-69-28-1	10/22/63	0757	1°47' S	172°05' W	-	-	-	-	-	-	4	-	-	3	7	3.6-10.0
Do.	do.	0	G-69-36-1	10/24/63	2000	8°10' S	169°27' E	-	-	-	-	-	-	-	1	-		1	4.4
Do.	do.	0	G-69-75-1	11/22/63	1357	12°37' S	178°12' W	-	-	-	-	-	-	6	-	-	-	6	7.4-10.8
Do.	do.	0	E-3-42	3/8/64	1930	15°32' N	170°32' W	-	-	1920	-	-	-	2	-	-	-	2	6.0, ca. 6.4
Do.	do.	0	E-3-86	3/13/64	1939	16°50' N	172°03' W	-	-	3169	-	-	-	-	-	-	1	1	ca. 4.2
Do.	do.	0	E-5-16	5/9/64	1815	13°20' N	171°02' W	-	-	1657	-	-	-	4	2	-	-	6	4.9-8.6
Do.	do.	0	E-5-36	5/11/64	1815	14°24' N	172°38' W	-	-	1163	-	-	-	1	-	-	-	1	10.3
Do.	do.	0	E-5-53	5/13/64	1817	15°01' N	174°14' W	-	-	1516	-	-	-	-	1	-	-	1	9.2
Do.	do.	0	E-5-59	5/14/64	1815	16°52' N	171°19' W	-	-	1785	-	-	-	2	-	1	-	3	BL 3.9-ca. 6.0, BB
Do.	do.	0	E-6-17	6/8/64	1926	15°34' N	169°14' W	-	-	1063	-	-	-	3	-	-	-	3	ca. 7.0-7.8
Do.	do.	0	E-6-37	6/10/64	1923	14°17' N	170°13' W	-	-	1294	-	-	-	1	-	-	-	1	5.9
Do.	do.	0	E-6-61	6/12/64	1927	15°03' N	171°49' W	-	-	1271	-	-	-	5	-	-	1	6	3.6-7.7

Appendix Table 1.--Record of catches of istiophorid larvae and juveniles by the Southwest Fisheries Center, Honolulu Laboratory from 1950 to 1971.--Continued.

Gear	Type of tow	Depth of tow	Vessel[1]/ cruise station sample	Date	Time	Position		Duration of tow		Volume of water strained	Surface temperature	Surface salinity	Larval and juvenile catches[2]						Size range
						Latitude	Longitude						SF	BL	SB	BB	UN	Total	
								Hr.	Min.	m³	° C	°/₀₀							mm
1-m plankton net	horizontal	0	E-6-80	6/14/64	1954	15°53' N	173°27' W	-	-	1455	-	-	-	5	-	1	-	6	BL 5.5-8.6, BB 23.0
Do.	do.	0	E-6-84	6/15/64	1922	18°27' N	170°53' W	-	-	-	-	-	-	-	1	-	-	1	4.9
Do.	do.	0	C-2-13	3/29/64	2003	14°37' N	147°58' W	-	-	678?	24.0	34.48	-	1	-	-	-	1	5.2
Do.	do.	0	C-3-13	4/27/64	2020	14°00' N	147°55' W	-	-	1839	24.8	34.52	-	1	-	-	-	1	6.5
Do.	do.	0	C-4-9	5/25/64	2003	20°28' N	151°04' W	-	-	1413	22.9	35.09	-	-	1	-	-	1	24.2
Do.	do.	0	C-4-10	5/26/64	2002	16°29' N	150°58' W	-	-	1588	24.2	34.53	-	-	1	-	-	1	3.8
Do.	do.	0	C-6-10	7/22/64	2000	17°18' N	151°01' W	-	-	2192	25.8	34.78	-	1	1	-	-	2	BL 6.0, SB 3.8
Do.	do.	0	C-6-14	7/26/64	2005	17°03' N	147°58' W	-	-	1515	26.0	34.46	-	1	-	-	-	1	5.8
Do.	do.	0	C-15-6	4/16/65	2000	16°10' N	154°00' W	-	-	2060	25.6	34.32	-	-	4	-	-	4	4.0-4.4
Do.	do.	0	C-15-10	4/20/65	2004	17°07' N	150°59' W	-	-	2573	24.8	34.42	-	-	2	-	-	2	4.6, ca. 4.8
Do.	do.	0	C-16-3	5/27/65	2007	12°58' N	157°04' W	-	-	1488	26.1	-	-	1	-	-	-	1	5.0
Do.	do.	0	C-46-23-3	10/21/69	0100	7°26' N	144°43' W	-	-	1333	28.4	33.84	-	1	-	-	-	1	5.2
Do.	do.	0	C-46-27-1	10/22/69	2100	7°29' N	145°05' W	-	-	1614	28.8	33.99	-	-	2	-	-	2	3.3, 3.8
Do.	do.	0	C-46-27-2	10/22/69	2300	7°29' N	145°05' W	-	-	1837	28.8	33.99	-	-	1	-	-	1	3.5
Do.	do.	0	C-46-29-2	10/23/69	2300	7°28' N	145°14' W	-	-	1535	28.9	33.85	-	-	1	-	-	1	ca. 2.8
Do.	do.	0	C-46-29-3	10/24/69	0100	7°28' N	145°14' W	-	-	1592	28.8	33.84	-	-	1	-	-	1	3.8
Do.	do.	0	C-46-31-1	10/24/69	2100	7°31' N	145°02' W	-	-	1734	28.9	33.84	-	-	1	-	-	1	3.8
Do.	do.	0	C-46-31-2	10/24/69	2300	7°31' N	145°02' W	-	-	1516	28.8	33.84	-	-	1	-	-	1	3.9
Do.	do.	0	C-46-31-3	10/25/69	0100	7°31' N	145°02' W	-	-	1536	28.8	33.91	-	2	1	-	-	3	4.3-4.5
Do.	do.	0	C-48-46-1	4/15/70	2300	3°22' N	144°56' W	-	-	1744	28.5	34.81	-	-	-	1	-	1	ca. 5.8
Do.	do.	0	C-48-79-1	4/23/70	2100	3°32' S	144°56' W	-	-	1268	28.8	34.92	-	-	-	1	-	1	6.6
Do.	oblique	0-40	S-21-30-1	8/14/53	0240	21°03' N	157°31' W	-	-	1954	26.1	35.16	-	1	-	-	-	1	4.5
Do.	do.	0-60	S-35-8-1	8/2/56	1455	21°12' N	158°22' W	-	-	1641	26.2	-	-	-	1	-	-	1	4.8
Do.	do.	0-60	S-38-64-2	3/5/57	2030	17°56' S	140°28' W	-	-	533	-	-	-	1	-	-	-	1	3.0
Do.	do.	0-60	S-47-14-1	10/19/58	0502	17°40' N	154°34' W	-	-	1253	26.3	34.72	-	1	-	-	-	1	5.5
Do.	do.	0-60	S-50-2	1/11/59	2008	14°42' N	152°21' W	-	-	1154	24.8	34.74	-	-	1	-	-	1	7.2
Do.	do.	0-60	S-50-33	2/3/59	2004	15°52' N	169°54' W	-	-	1394	24.8	34.83	-	-	2	-	-	2	5.9, 6.3
Do.	do.	0-60	G-41-169-1	8/19/58	2331	21°10' N	158°19' W	-	-	1749	26.7	34.91	-	-	1	-	-	1	5.2
Do.	do.	0-60	G-44-24-1	5/21/59	2003	18°03' N	161°03' W	-	-	1458	26.1	34.34	-	-	1	-	-	1	ca. 4.0
Do.	do.	0-60	G-44-32-1	5/30/59	2004	18°03' N	155°14' W	-	-	-	-	-	-	-	2	-	-	2	4.5, 5.1
Do.	do.	0-60	G-45-14-1	7/19/59	2032	20°40' N	163°42' W	-	-	1034	26.7	34.26	-	1	-	-	-	1	5.9
Do.	do.	0-60	G-45-15-1	7/20/59	2030	23°20' N	166°10' W	-	-	1055	26.4	34.70	-	1	-	-	-	1	9.4
Do.	do.	0-60	G-45-22-1	7/24/59	2024	23°07' N	159°00' W	-	-	811	26.7	34.37	-	1	-	1	1	3	BL 4.0, UN 4.2, BB7.5
Do.	do.	0-60	G-45-29-1	7/29/59	1958	16°48' N	154°38' W	-	-	1284	25.9	-	-	-	-	1	-	1	?
Do.	do.	0-60	G-46-16-B	10/4/59	2034	22°48' N	153°42' W	-	-	1466	-	-	-	-	-	-	1	1	ca. 3.5
Do.	do.	0-60	G-46-21-A	10/10/59	2002	15°33' N	160°15' W	-	-	1421	26.9	34.53	-	-	-	-	1	1	ca. 5.0
Do.	do.	0-60	G-46-23-A	10/12/59	2004	18°08' N	164°57' W	-	-	1397	27.4	34.31	-	1	-	-	-	1	6.8
Do.	do.	0-60	G-52-79-1	4/20/61	0214	18°21' N	168°53' W	-	-	1498	25.4	34.72	-	1	-	-	-	1	4.3
Do.	do.	0-60	G-53-3-1	6/24/61	1130	19°04' N	155°59' W	-	-	1947	26.4	34.51	-	1	1	-	1	3	BL 4.8, SB 3.9, UN 4.3
Do.	do.	0-60	M-35-27-1	5/13/57	1716	22°20' N	157°46' W	-	-	1677	23.4	35.08	-	-	-	1	-	1	ca. 9.8
Do.	do.	0-140	S-43-88-1	2/20/58	2010	7°49' N	148°37' W	-	-	1506	27.8	-	-	1	-	-	-	1	3.9
Do.	do.	0-140	S-45-98-1	5/24/58	0314	6°34' S	139°41' W	-	-	1426	27.9	35.02	-	1	-	-	-	1	4.0
Do.	do.	0-140	S-45-158-1	6/21/58	2010	17°14' N	153°40' W	-	-	1951	25.1	-	-	-	-	1	-	1	6.9
Do.	do.	0-140	S-46- 1	7/22/58	2127	23°56' N	158°28' W	-	-	1623	25.4	-	-	2	-	-	1	3	4.4-6.9
Do.	do.	0-140	G-48-18	6/30/60	0600	17°06' N	173°51' W	-	-	-	27.2	-	-	2	-		-	2	6.0, 6.1

Appendix Table 1.--Record of catches of istiophorid larvae and juveniles by the Southwest Fisheries Center, Honolulu Laboratory from 1950 to 1971.--Continued.

Gear	Type of tow	Depth of tow	Vessel[1]/ cruise/ station sample	Date	Time	Position		Duration of tow		Volume of water strained	Surface temperature	Surface salinity	Larval and juvenile catches[2]						Size range
						Latitude	Longitude						SF	BL	SB	BB	UN	Total	
								Hr.	Min.	m³	° C	°/°°							mm
1-m plankton net	oblique	0-140	G-48-35	7/7/60	1801	12°53' N	174°28' E	-	-	-	27.8	-	-	1	-	-	-	1	4.6
Do.	do.	0-140	G-48-54	7/22/60	0600	11°34' N	159°54' E	-	-	-	28.7	-	-	-	-	-	1	1	4.9
Do.	do.	0-140	G-48-104	8/16/60	1800	24°15' N	178°54' E	-	-	-	29.0	-	-	1	-	-	-	1	4.5
Do.	do.	0-140	G-55-26-1	1/29/62	1358	9°40' S	171°38' E	-	-	-	29.2	-	-	1	-	-	-	1	4.9
Do.	do.	0-140	G-55-39-1	2/10/62	0808	23°29' S	168°04' E	-	-	-	25.8	-	-	1	1	-	-	2	BL 8.6, SB 12.8
Do.	do.	0-140	G-55-97-2	3/12/62	0804	18°14' S	172°07' W	-	-	-	27.8	-	-	1	-	-	-	1	5.1
Do.	do.	0-140	G-69-11-2	10/13/63	0759	9°11' N	171°48' W	-	-	-	-	-	-	1	-	-	-	1	3.4
Do.	do.	0-140	G-69-26-2	10/21/63	2002	0°02' S	172°31' E	-	-	-	-	-	-	1	-	-	-	1	4.3
Do.	do.	0-150	S-6-19-3	8/20/50	2311	19°31' N	157°10' W	-	-	4782	26.0	-	-	1	-	-	-	1	21.2
Do.	do.	0-200	S-5-7	7/4/50	1649	15°00' N	171°54' W	-	-	888	26.7	34.56	-	1	-	-	-	1	4.3
Do.	do.	0-200	S-17-21	9/11/52	1930	20°28' N	155°37' W	-	-	1679	25.5	35.05	-	-	1	-	-	1	6.4
Do.	do.	0-200	S-34-7	4/30/56	1540	16°31' N	153°58' W	-	-	2286	24.8	34.42	-	-	1	-	-	1	6.7
Do.	do.	0-200	S-34-136	6/28/56	1402	21°02' N	160°26' W	-	-	1927	25.2	34.92	-	1	-	-	-	1	6.3
Do.	do.	0-200	S-35-101	8/30/56	0803	10°47' S	143°01' W	-	-	1576	26.1	-	-	-	1	-	-	1	7.1
Do.	do.	0-200	S-35-137	9/11/56	0807	16°45' S	149°52' W	-	-	1537	25.9	-	-	-	-	1	1	2	?
Do.	do.	0-200	S-35-158	9/24/56	2110	5°52' S	160°03' W	-	-	1876	26.7	-	-	-	1	-	-	1	4.5
Do.	do.	0-200	S-35-168	9/29/56	2117	4°24' N	160°08' W	-	-	1687	26.9	34.81	-	-	-	1	-	1	?
Cobb trawl	horizontal	15-20	C-32-19	7/20/67	1944	20°59' N	158°30' W	6	0	-	28.0	-	-	1	-	-	-	1	9.2
Do.	do.	8-60	C-32-29	7/26/67	0343	21°00' N	158°32' W	4	12	-	26.0	-	-	2	-	-	-	2	16.6, 18.5
Do.	do.	14-20	C-32-66	9/15/67	0345	19°45' N	156°06' W	6	0	-	28.0	-	-	3	-	-	-	3	13.0-19.5
Do.	do.	87-119	C-32-67	9/15/67	1152	19°53' N	156°05' W	6	0	-	28.3	-	-	1	-	-	-	1	18.9
Do.	do.	13-18	C-32-70	9/16/67	1946	19°24' N	156°00' W	6	0	-	28.3	-	-	2	-	-	-	2	8.6, 10.6
Do.	do.	9-18	C-32-81	9/23/67	1941	21°22' N	158°14' W	6	0		27.5	-	-	1	-	-	-	1	9.8
Do.	do.	20	C-46-25	10/21/69	1948	7°26' N	144°42' W	-	-	-	28.6	-	-	2	-	-	-	2	ca. 12.0, 16.3
Do.	do.	50	C-53-54	4/24/71	1832	19°11' N	147°27' E	2	0	-	28.6	-	-	2	-	-	-	2	22.0, 24.1
Do.	do.	100	C-55-53	11/7/71	0030	21°03' N	147°54' E	2	55	-	28.7	-	-	4	-	-	-	4	20.0-55.0
Neuston net	do.	0	C-55-5	10/24/71	1229	21°52' N	173°05' W	-	30	-	27.8	-	-	-	1	-	-	1	9.2
Do.	do.	0	C-55-13	10/29/71	1230	22°30' N	168°22' E	-	30	-	-	-	-	3	-	-	-	3	5.5-6.1
Do.	do.	0	C-55-21	11/2/71	1230	22°52' N	149°06' E	-	30	-	-	-	-	1	-	-	-	1	10.0
Do.	do.	0	C-55-92	11/12/71	1230	16°17' N	149°16' E	-	30	-	-	-	-	1	-	-	-	1	4.5
Do.	do.	0	C-55-106	11/23/71	1230	6°50' N	163°36' E	-	30	-	-	-	-	2	-	-	-	2	6.7, 9.2
Do.	do.	0	C-55-132	12/1/71	1230	8°07' N	171°14' E	-	30	-	28.7	-	-	17	-	-	-	17	6.6-20.0

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[1] S = Hugh M. Smith, G = Charles H. Gilbert, E = U.S.S. Energy, C = Townsend Cromwell, M = John R. Manning.

Appendix Table 2.--Record of catches of swordfish larvae and juveniles by Southwest Fisheries Center, Honolulu Laboratory from 1950 to 1971.

Gear	Type of tow	Depth of tow	Vessel cruise no.[1]	Station/ no. of samples	Date	Time (local)	Position Latitude	Position Longitude	Volume of meter	Surface temperature	Surface salinity	Size range (SL)
									m³	°C	‰	mm
1-m plankton net	Horizontal	0	S-4	15-1	5/21/50	1610	20°13' N	158°30' W	2950	24.5	--	10.5; 19.3
Do.	do.	0	S-4	20-1	5/23/50	0911	20°14' N	157°04' W	3346	23.6	--	6.6
Do.	do.	0	S-4	23-1	5/14/50	1852	22°40' N	157°10' W	2192	23.3	--	9.6
Do.	do.	0	S-39	21-1	5/9/57	2010	23°03' N	165°23' W	--	25.1	35.21	7.3; 8.8; 11.6; 13.4; 15.8
Do.	do.	0	S-39	28-1	5/15/57	2010	20°03' N	162°04' W	--	25.1	34.96	6.5; ca. 7.0; 19.6
Do.	do.	0	E-5	59-1	5/14/64	1815	16°52' N	171°19' W	1785	--	--	8.3
Do.	do.	0	E-6	80-1	6/14/64	1954	15°53' N	173°27' W	1455	--	--	23.0
Do.	do.	0	C-48	46-1	4/15/70	2300	3°22' N	144°56' W	1744	28.5	34.81	5.8
Do.	do.	0	C-48	79-1	4/23/70	2100	3°32' S	144°56' W	1268	28.8	--	6.6
Do.	Oblique	60	M-35	27-1	5/13/57	1716	22°20' N	157°46' W	1677	23.4	35.08	9.8
Do.	do.	60	G-45	22-1	7/24/59	2024	23°07' N	159°00' W	811	26.7	34.37	7.5
Do.	do.	140	S-45	158-1	6/21/58	2010	17°14' W	153°40' W	1951	25.1	--	6.9
Do.	do.	200	S-35	137-1	9/11/56	0807	16°45' S	149°52' W	1537	25.9	--	ca. 8.0 (head only)

[1] C = *Townsend Cromwell*, E = U.S.S. *Energy*, G = *Charles H. Gilbert*, M = *John R. Manning*, S = *Hugh M. Smith*.

DEVELOPMENT AND DISTRIBUTION OF LARVAE AND JUVENILES OF *SEBASTOLOBUS* (PISCES; FAMILY SCORPAENIDAE)

H. Geoffrey Moser[1]

ABSTRACT

The North Pacific scorpaenid genus *Sebastolobus* is composed of three deepwater coastal species of potential commercial importance. They are oviparous and produce bilobed gelatinous egg sacs that float to the surface waters where hatching and larval development occur. Transformation into pelagic juveniles occurs at about 20 mm length. The pelagic stage of *S. alascanus* is relatively short-lived, as they transform into benthic juveniles at 22 to 27 mm length. In the deep-living *S. altivelis* the juveniles remain pelagic for well over a year and grow as large as 56 mm.

Larvae of the two species mentioned are collected regularly on plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and pelagic and benthic juveniles are common constituents of mid-water and bottom trawls taken in the CalCOFI region. In this paper specimens from these sources are used to describe the larval and juvenile stages of the two species and to show the striking morphological changes which occur during development. Also presented are data on geographic distribution and patterns of seasonal abundance of larvae. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species.

Knowledge of the life history of the scorpionfish genus *Sebastolobus* is scanty. Pearcy (1962) described the floating egg masses, the developing embryos, and the newly hatched larvae of *Sebastolobus*. The larvae of *Sebastolobus* occur in the plankton collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and can be differentiated from those of *Sebastes* on the basis of the spination of the parietal ridge (Ahlstrom, 1961). Information on the distribution and abundance of *Sebastolobus* larvae in CalCOFI has hitherto not appeared in the literature, nor has a description of the larval stages. It is the purpose of this paper to fill that void and also to describe the distinctive juvenile stages of *S. altivelis* and *S. alascanus,* which are common constituents of mid-water trawl catches in the eastern North Pacific.

The three known species of *Sebastolobus* inhabit the coastal waters of the North Pacific. *Sebastolobus altivelis* ranges from the southern tip of Baja California to the Aleutian Islands while *S. alascanus* is found from northern Baja California to the Bering Sea and the Commander Islands off the Asiatic mainland. The Asian species, *S. macrochir,* ranges from the coast of Japan northward to the Bering Sea south of Cape Navarin and into the Sea of Okhotsk (Barsukov, 1964). At present the commercial catch of *Sebastolobus* is small, however, data of Best (1964) and Alverson, Pruter, and Ronholt (1964) suggest that these fishes may constitute a substantial resource in the deep coastal waters of the northeast Pacific.

The taxonomic characters of the adult members of this genus have been reviewed by a number of investigators (Starks, 1898; Hubbs, 1926; Matsubara, 1943; Phillips, 1957; Barsukov, 1964; Miller and Lea, 1972). *Sebastolobus* is distinguished from other scorpaenid genera by the unusual pectoral fins, each of which is separated by a notch into dorsal and ventral lobes, by possessing more vertebrae (28 to 31) and dorsal spines (15 to 17), a complete set of circumorbital bones, an uppermost pectoral radial which is free from the scapula, and by a suborbital stay with a broad posterior end anchored firmly onto the preopercular bone. The two North American species may be separated on the basis of the shape and number of rays in the spinous dorsal fin. In *S. altivelis* the third spine is the longest while in *S. alascanus* the fourth or fifth spine is the longest. The former species usually has 15 (rarely 16) spinous dorsal rays while the latter has 16 or 17 (rarely 15) rays. Also, *S. altivelis* usually has 29 (rarely 28) vertebrae and *S. alascanus* has 30 (rarely 31). The Asian species, *S.*

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macrochir, is deeper bodied than the North American species and has a relatively narrower caudal peduncle. Counts of its spinous dorsal rays and vertebrae are close to those of *S. altivelis.*

Hubbs (1926), Barsukov (1964), and Miller and Lea (1972) have given information on the bathymetric ranges of the adults. In summary, *S. altivelis* occurs typically at 550 to 1,300 m with known depth extremes of 200 to 1,550 m. Everywhere along its latitudinal range *S. altivelis* is deeper living than *S. alascanus,* although there is some overlap and the two species are occasionally taken in the same trawls. *Sebastolobus alascanus* commonly occurs at 180 to 440 m, with known depth extremes of 18 to 1,524 m. *Sebastolobus macrochir* occurs commonly at 400 to 640 m.

MATERIALS AND METHODS

Larvae of *Sebastolobus* from 2 yr (1960, 1966) of CalCOFI survey cruises were identified and counted. From these a developmental series that encompassed the entire larval period was established. Larvae of this series were measured with the ocular micrometer of a stereoscopic microscope, according to the methods of Moser (1967, 1972), to produce the tables of morphometrics (Tables 1-3) needed for comparison of body proportions of *S. altivelis* and *S. alascanus.* This series also provided the specimens needed to describe the general morphology and melanophore pattern of the larvae. Measurements of four pelagic juveniles of *S. macrochir* are given in Table 4. An abbreviated series of *S. altivelis* and *S. alascanus* was selected, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S to produce tables of meristics (Tables 5, 6).

The pelagic juvenile stages of the two species were obtained from the mid-water trawl collections of the Los Angeles County Museum of Natural History (LACM), the Scripps Institution of Oceanography (SIO), and the Southwest Fisheries Center. Demersal juveniles were obtained from otter trawl collections of LACM and SIO. As for larvae, series of juveniles were established for analysis of morphometrics (Tables 2-4), pigment pattern, and meristic characters (Tables 5, 6). In this paper the term "body length" refers to the distance from the snout to the tip of the notochord in larvae which have not yet formed the caudal fin. After dorsad flexion of the tip of the notochord and completion of caudal fin formation "body length" refers to standard length (distance from snout to posterior edge of hypural plate).

TABLE 1.—Measurements (mm) of *Sebastolobus* spp. larvae. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
3.0	1.3	0.50	0.08	0.20	0.60	0.3	0.14			
3.5	1.4	0.80	0.18	0.25	0.52	0.23	0.20			
3.8	1.6	1.0	0.22	0.27	0.68	0.40	0.38			
4.2	1.8	1.2	0.25	0.30	0.86	0.45	0.40			
4.7	1.9	1.2	0.31	0.30	0.80	0.46	-			
5.0	2.0	1.4	0.35	0.33	0.90	0.65	0.50			
5.2	2.1	1.4	0.43	0.40	1.0	0.62	0.55			
5.5	2.3	1.6	0.42	0.35	1.1	0.65	0.58			
5.7	2.3	1.7	0.56	0.40	1.2	0.95	0.85			
5.8	2.4	1.7	0.51	0.39	1.2	1.0	0.78			
5.9	2.6	1.8	0.62	0.47	1.6	1.0	0.75			
6.0	2.7	1.8	0.55	0.51	1.8	1.3	0.85	0.22	2.3	3.4
6.2	2.7	1.9	0.70	0.48	1.6	1.4	0.90	0.20	-	-
6.4	2.7	1.8	0.60	0.45	1.5	1.2	0.85	0.13	-	-
6.7	3.1	1.9	0.82	0.55	1.8	1.4	1.0	0.15	3.9	3.9
6.8	2.8	2.0	0.82	0.52	1.8	1.4	1.1	0.17	-	3.2
6.9	3.3	2.2	0.80	0.58	2.0	1.5	1.2	0.25	2.7	4.1
7.1	3.5	2.5	0.82	0.71	2.4	1.8	1.2	0.80	2.5	4.2
7.3	3.8	2.5	0.95	0.76	2.4	1.8	1.4	0.85	2.7	4.4
7.7	4.2	2.7	1.1	0.75	2.8	2.1	1.5	0.85	2.9	4.5
7.8	4.3	3.1	1.1	0.82	2.6	2.1	1.4	1.2	3.2	4.8
8.3	4.4	3.1	1.1	0.79	2.6	2.0	1.4	1.0	3.1	4.9
8.6	4.8	3.2	1.2	0.92	3.1	2.4	1.7	1.4	3.5	5.3
8.9	5.2	3.3	1.2	1.0	3.1	2.5	1.7	1.4	3.8	5.4
9.2	5.2	3.5	1.2	1.0	3.2	2.7	1.5	1.5	3.8	5.6
9.6	5.4	3.5	1.2	1.1	3.7	2.8	1.8	1.7	4.1	5.8

TABLE 2.—Measurements (mm) of *Sebastolobus altivelis*. Specimens below dashed line have completed transformation into pelagic juvenile stage.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
10.1	6.2	3.8	1.2	1.2	3.8	2.8	1.8	1.7	4.2	6.4
10.5	6.5	4.2	-	1.2	3.9	3.0	1.9	1.8	4.4	6.7
11.2	6.9	4.5	1.3	1.4	4.2	3.5	2.1	2.4	5.2	7.3
12.7	7.3	4.6	1.3	1.5	4.7	3.8	2.0	2.5	5.4	7.9
13.4	8.0	5.0	1.5	1.6	4.8	3.7	2.0	2.5	5.4	8.3
14.4	8.8	6.2	1.7	2.1	5.7	5.0	2.7	3.1	6.0	9.6
15.2	10.1	6.1	1.8	1.9	6.3	5.2	2.8	2.9	6.7	10.6
15.4	9.8	6.0	1.7	2.2	6.4	4.7	2.8	2.9	6.9	10.1
15.4	9.9	6.5	1.9	2.2	6.3	5.8	2.9	3.8	6.8	11.0
15.7	10.3	6.8	2.1	2.1	6.9	5.8	2.9	3.8	6.7	10.8
16.0	10.3	6.2	1.8	2.0	7.1	5.4	3.1	3.3	7.0	10.6
16.3	10.3	7.2	2.1	2.2	6.6	6.2	3.0	4.0	6.8	11.2
16.6	10.8	7.4	1.8	2.4	6.6	6.4	3.0	3.4	7.6	11.8
16.7	11.2	6.7	1.9	2.2	7.5	5.8	3.2	3.3	7.1	11.3
17.6	11.5	7.6	2.0	2.5	7.2	6.8	3.2	4.2	7.1	12.2
17.6	11.7	7.0	1.9	2.4	7.3	5.9	3.1	3.8	7.7	12.0
18.2	12.0	7.7	2.1	2.6	7.3	6.3	3.1	4.2	7.8	12.7
18.4	12.5	7.1	2.0	2.5	8.3	6.2	3.6	4.2	7.5	12.8
19.3	13.2	7.9	2.1	2.5	8.5	6.7	3.8	3.8	8.3	13.4
19.4	13.0	8.5	2.3	2.5	8.7	7.6	3.8	4.7	8.4	14.0
20.7	13.8	8.5	2.6	2.3	8.4	7.6	3.7	4.8	8.6	14.7
21.3	14.9	9.2	2.8	2.8	9.0	8.1	3.8	4.8	9.5	15.2
22.6	15.9	9.6	2.5	3.1	9.2	8.8	4.2	5.6	9.5	16.7
23.4	16.6	9.8	2.5	2.7	10.1	9.0	4.4	5.6	9.5	17.4
24.5	17.7	10.8	2.9	3.4	11.0	10.0	4.5	5.8	10.1	18.1
25.8	18.6	10.6	2.9	2.9	11.3	9.3	4.4	5.9	10.1	18.9
26.8	17.7	10.6	2.8	3.8	10.6	11.0	4.8	6.5	10.1	18.8
27.7	20.3	11.5	2.9	3.6	12.2	11.0	5.4	7.1	11.7	22.0
28.3	20.3	12.0	3.2	3.7	12.2	11.5	5.0	7.1	11.5	21.8
29.4	20.4	12.3	3.3	3.8	11.5	11.5	5.2	7.2	12.3	21.1
30.5	21.1	13.0	3.8	3.6	11.7	11.7	5.4	7.6	12.3	23.0
31.4	21.1	12.3	3.2	3.5	13.7	12.2	5.8	7.5	12.3	22.9
32.4	21.1	12.5	3.5	3.6	13.0	12.8	5.8	8.3	12.5	22.2
33.6	23.1	14.0	4.2	4.2	13.5	11.7	5.8	7.5	12.8	25.1
34.6	23.5	13.4	3.8	3.8	14.2	13.5	6.0	8.2	13.7	25.5
36.5	25.0	15.2	4.2	4.8	15.5	14.7	6.7	9.2	14.9	27.5
37.5	25.8	15.0	4.2	4.6	15.9	14.4	6.7	8.3	14.7	27.6
38.5	25.6	15.2	4.0	4.8	16.0	15.7	6.6	9.8	15.2	27.5
39.5	27.9	16.2	5.0	4.8	16.0	15.0	6.7	8.9	16.0	29.9
40.4	27.1	16.4	5.0	4.8	15.2	15.0	6.8	10.8	16.0	30.0
41.6	27.9	16.4	4.3	5.8	15.9	15.2	7.1	10.1	16.2	29.6
42.3	28.1	16.9	4.6	5.2	17.4	15.2	7.2	10.0	15.9	29.4
43.5	30.1	16.9	5.2	5.4	16.0	14.7	6.7	9.5	17.4	32.4
44.4	30.0	17.9	-	4.8	16.4	16.4	7.1	9.5	17.2	32.2
45.1	29.5	18.2	4.8	5.4	17.6	16.0	7.8	10.1	17.2	32.0
46.2	30.7	17.9	5.0	4.9	17.7	17.1	8.1	11.5	17.1	33.5
47.1	30.2	18.1	5.0	5.6	17.1	15.2	7.0	10.3	17.7	33.0
48.5	32.0	18.6	5.4	5.8	18.6	16.9	7.8	10.5	17.7	34.7
49.5	32.2	19.8	5.0	5.8	18.6	18.1	8.3	11.8	16.4	36.2
51.3	37.0	20.6	6.7	5.8	18.8	17.4	8.0	11.3	18.9	40.0
53.5	35.7	20.6	6.2	7.5	18.6	16.9	8.2	11.0	18.7	37.8
56.0	37.6	21.4	5.8	7.7	19.2	19.8	8.3	12.3	20.3	40.6
*42.0	26.8	16.6	4.6	5.6	12.0	12.7	6.0	9.3	16.4	29.0
*47.4	29.6	17.7	4.7	6.9	13.9	13.5	6.8	10.1	18.1	31.7
*48.1	31.4	19.1	5.2	7.3	14.4	15.2	7.0	11.5	17.9	33.5
*50.3	33.0	19.2	5.4	7.3	14.0	13.8	7.1	11.8	18.8	35.3
*51.0	33.0	19.5	4.7	7.2	15.0	16.2	7.5	11.2	18.7	35.2
*53.0	33.4	20.5	5.4	8.6	14.6	15.5	7.0	12.1	19.9	37.7
*54.0	35.4	19.7	5.9	7.3	15.5	17.7	7.8	12.6	20.6	38.4
*56.0	35.2	21.1	5.6	7.7	15.5	16.4	7.4	12.6	20.8	38.1
*57.5	37.2	21.4	5.6	8.0	15.3	16.7	8.1	12.5	21.1	40.3
*58.6	37.9	22.6	6.0	8.7	16.5	16.9	8.2	12.7	21.6	40.6
*60.0	38.0	22.0	6.0	8.4	16.2	15.1	8.1	12.8	21.5	41.6

*Benthic juvenile.

TABLE 3.—Measurements (mm) of larvae and juveniles of *Sebastolobus alascanus*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout anal fin
10.3	6.2	4.2	1.5	1.2	4.0	3.2	1.6	1.9	4.3	6.8
11.2	7.4	5.0	1.8	1.3	4.1	3.2	1.7	2.1	5.0	7.7
11.7	7.2	5.0	-	1.3	3.9	3.1	1.8	2.1	5.1	7.7
12.5	7.7	4.7	1.7	1.5	4.5	3.6	1.8	2.4	5.4	8.3
13.2	7.3	5.0	1.6	1.8	4.6	3.9	1.9	2.7	5.8	8.2
14.0	8.1	5.7	1.8	2.1	4.9	4.1	1.9	2.5	6.2	8.8
14.4	8.4	5.6	1.4	1.8	5.2	4.2	2.1	2.6	5.7	9.1
15.2	9.2	6.2	1.8	2.0	5.2	4.4	2.1	2.9	6.3	10.0
16.0	9.3	6.2	2.0	2.0	5.2	4.8	2.2	2.9	7.1	10.0
16.4	9.8	6.7	1.8	2.5	5.7	4.7	2.3	3.2	7.1	10.5
16.9	10.0	6.8	1.9	2.3	5.9	4.8	2.4	3.1	7.3	10.8
17.6	10.6	6.7	2.1	2.2	6.1	4.9	2.3	3.5	7.1	11.3
18.6	12.7	-	-	2.8	6.8	5.4	2.8	3.8	8.5	13.2
19.8	12.0	7.7	2.0	2.8	7.1	5.9	2.9	4.0	8.3	13.0
20.0	12.0	8.1	2.2	2.9	7.1	6.4	2.8	4.2	8.4	13.0
20.3	12.8	8.2	1.8	3.1	7.2	6.2	7.8	4.0	8.1	13.5
21.0	13.5	8.6	1.9	3.1	7.5	6.5	3.0	4.6	8.1	14.4
21.4	12.8	8.3	2.4	2.9	7.1	6.2	2.8	3.8	8.6	14.4
21.9	12.8	8.5	2.1	3.1	7.1	6.2	2.8	4.2	8.8	14.9
22.3	14.2	9.6	-	2.8	7.9	6.5	3.2	4.4	9.1	15.4
22.9	14.4	9.8	2.6	3.2	7.5	6.7	3.1	4.6	9.3	15.5
23.2	14.7	9.5	2.5	2.9	7.9	7.2	3.0	5.0	9.6	16.0
23.4	14.9	9.0	2.2	3.3	8.0	7.1	3.2	5.0	9.3	16.4
24.0	14.4	9.8	2.2	3.2	8.0	6.8	3.3	5.0	9.8	15.9
24.3	15.5	10.0	2.8	3.2	8.6	7.3	3.3	5.0	9.8	16.9
25.1	15.9	10.0	3.0	3.3	8.4	7.0	3.4	5.0	10.1	17.2
25.5	16.0	10.1	2.8	3.5	8.8	8.2	3.7	5.5	10.1	17.6
26.4	17.9	10.6	3.2	3.5	9.0	8.0	3.7	5.7	11.3	19.1
27.2	17.9	11.2	3.0	-	8.3	8.1	3.3	5.4	10.8	19.3
*22.5	13.0	8.7	2.1	3.2	7.2	6.3	2.9	4.6	9.6	14.7
*25.3	16.9	10.3	3.5	3.2	8.1	6.8	3.3	5.0	11.2	18.9
*37.8	22.0	12.7	2.9	5.0	10.1	9.6	4.2	8.2	13.5	24.3
*39.0	24.0	14.1	4.0	5.1	9.9	9.8	4.0	8.8	15.0	26.7
*40.8	25.1	14.8	3.8	5.3	10.0	9.7	3.8	8.8	15.3	27.3
*42.3	27.7	15.4	4.3	5.8	10.1	10.0	4.2	9.0	16.3	29.6
*43.6	26.3	15.4	4.1	5.8	9.5	10.6	4.4	9.4	16.1	29.5
*44.7	26.2	15.9	4.3	5.8	11.2	10.5	4.8	8.1	16.9	29.7
*46.2	28.1	16.2	4.4	6.4	10.8	10.8	4.7	9.9	16.7	31.2
*48.8	29.1	16.8	4.7	6.5	11.4	11.4	4.7	10.5	18.0	32.9
*50.3	29.4	17.4	4.8	7.0	12.4	12.2	5.0	10.6	18.0	33.0
*51.0	30.6	17.5	5.0	6.8	11.8	11.5	5.2	10.5	17.5	33.6
*59.2	36.6	20.6	5.4	8.4	13.0	13.5	5.6	12.1	20.8	40.0
*60.0	36.8	21.6	5.7	9.0	14.3	14.3	5.9	13.0	21.5	39.7

* Benthic juvenile.

TABLE 4.—Measurements (mm) of pelagic juveniles of *Sebastolobus macrochir*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
21.0	14.5	9.2	2.5	3.1	9.1	9.2	3.8	5.4	10.0	15.0
25.5	17.9	10.8	3.0	4.5	11.2	11.2	4.7	7.1	11.3	18.2
27.2	18.6	11.8	3.8	4.3	12.5	11.0	4.8	7.7	12.2	19.1
29.8	19.2	13.2	3.0	5.0	13.2	13.2	5.7	8.5	13.5	20.8

TABLE 5.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus* spp. (above dashed line) and *Sebastolobus altivelis* (below dashed line).

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
6.2	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	-
6.8	-	-	-	-	3	3	14	2	-	-	-	3	-	-	-	-	-
7.0	8	7	-	-	5	5	14	12	-	-	-	2	-	-	-	-	-
7.7	8	7	4	4	7	7	23	24	2	1	3	9	III-5	XV-9	I-5	I-5	28
8.1	8	7	-	2	7	7	23	23	-	-	3	9	III-3	XV-9	I-5	I-5	28
8.3	8	7	3	4	7	7	23	23	2	1	2	8	III-5	XV-9	I-5	I-5	27
8.8	8	7	4	5	7	7	23	24	2	2	3	10	III-5	XV-9	I-5	I-5	29
9.3	8	7	3	4	7	7	24	24	2	1	3	10	III-5	XV-9	I-5	I-5	29
10.1	8	7	6	8	7	7	23	23	1	2	5	12	III-5	XV-9	I-5	I-5	29
10.6	7	7	6	7	7	7	23	23	1	2	5	13	III-6	XV-10	I-5	I-5	29
11.2	8	7	6	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	28
11.5	8	7	7	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	29
12.0	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-8	I-5	I-5	28
13.0	8	7	6	7	7	7	23	24	2	2	6	13	III-5	XV-10	I-5	I-5	29
13.7	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-9	I-5	I-5	29
14.4	8	7	7	7	7	7	23	24	2	2	6	14	III-5	XV-9	I-5	I-5	29
15.0	8	7	7	7	7	7	23	23	2	2	6	13	III-5	XV-9	I-5	I-5	29
16.6	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
17.6	8	7	8	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
18.1	8	7	7	7	7	7	24	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
19.4	8	7	7	7	7	7	22	22	2	2	6	14	III-5	XV-9	I-5	I-5	29
20.6	8	7	8	8	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
25.8	8	7	8	9	7	7	24	23	2	2	6	15	III-5	XV-9	I-5	I-5	29
30.5	8	7	6	7	7	7	24	24	2	2	7	15	III-5	XVI-9	I-5	I-5	29
40.4	8	7	7	7	7	7	23	23	2	2	7	15	III-5	XV-9	I-5	I-5	29
50.0	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-8	I-5	I-5	29

TABLE 6.—Meristics from cleared and stained larvae and juveniles of *Sebastolobus alascanus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
7.5	8	7	3	4	7	7	21	21	2	2	3	9	III-5	XVI-8	I-5	I-5	30
11.0	8	7	3	5	7	7	22	22	1	2	4	9	III-5	XVI-9	I-5	I-5	30
11.7	8	7	6	6	7	7	22	22	2	2	4	10	III-5	XVI-8	I-5	I-5	30
12.5	8	7	7	8	7	7	21	21	2	2	5	12	III-5	XVI-10	I-5	I-5	30
13.2	8	7	8	7	7	7	21	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
14.4	8	7	9	9	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	30
15.2	8	7	8	8	7	7	22	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
16.4	8	7	9	9	7	7	21	21	2	2	7	13	III-5	XVII-9	I-5	I-5	30
17.6	8	7	9	9	7	7	21	21	2	2	6	13	III-5	XVI-9	I-5	I-5	30
18.6	8	7	9	9	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
19.8	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
20.3	8	7	9	8	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	31
21.4	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
22.3	8	7	8	8	7	7	22	22	2	2	6	12	III-5	XVI-9	I-5	I-5	30
24.3	8	7	9	8	7	7	21	21	2	2	7	14	III-4	XVI-9	I-5	I-5	30
25.5	8	7	9	9	7	7	22	22	2	2	6	14	III-5	XV-10	I-5	I-5	30
26.4	8	7	9	9	7	7	21	21	2	2	7	12	III-5	XV-9	I-5	I-5	30
27.2	8	7	10	10			21	21	2	2	7	13	III-5	XVI-10	I-5	I-5	30

DESCRIPTION OF DEVELOPMENT

Distinguishing Features

Early *Sebastolobus* larvae (up to 6 mm) can be distinguished from those of all other genera of eastern Pacific Scorpaenidae on the basis of pigmentation. *Sebastolobus* larvae of this size range are unique in having two large melanistic blotches about midway along the tail, one at the dorsal midline and one at the ventral midline (Figure 1A, B). These are sometimes expanded to form a solid band on the tail. Early larvae of all other eastern Pacific scorpaenid genera have a series of melanophores along the ventral midline of the tail, and in some species of *Sebastes* an opposing row is present at the dorsal midline. The large tail blotches of *Sebastolobus* disappear in larvae between 5.0 and 6.5 mm. Soon after the loss of these large tail blotches in *Sebastolobus* the larvae develop prominent crestlike parietal ridges that terminate in double spines, the posterior (nuchal) spine being longer and more prominent than the anterior (parietal) spine (Figure 1F). Of the other eastern Pacific scorpaenid genera, only the larvae of *Scorpaenodes* have parietal ridges and spines like *Sebastolobus*. If two spines are present on the parietal ridges of other genera, the anterior spine is always longer and more prominent than the posterior. *Sebastolobus* larvae may be distinguished from those of *Scorpaenodes* on the basis of a melanistic shield, which covers the dorsolateral surface of the gut in the former and is absent in the latter. Larvae of *Sebastolobus* smaller than 10.0 mm could not be distinguished to species. Larvae larger than this can be identified to species by a combination of characters. The pectoral fins of *S. altivelis* larvae are relatively longer and are wider at the base than in *S. alascanus*. Also, larvae of *S. altivelis* are deeper bodied than those of *S. alascanus*. Details of the structural and pigmentary characters that differentiate the larvae and juveniles of the two species are given below.

General Morphology

Sebastolobus larvae hatch and are freed from their transparent gelatinous egg masses at about 2.6 mm (Pearcy, 1962). The smallest larvae in our plankton collections are about 3.0 mm long and still have the elliptical yolk sac with a posteriorly positioned oil droplet (Figure 1A). When the larvae reach approximately 3.5 mm, the yolk sac has been resorbed and the jaws and feeding apparatus are well formed (Figure 1B). Flexion of the notochord begins in larvae about 6.0 mm long and is completed in larvae about 7.5 mm (Figure 1E, F). Larvae larger than 10.0 mm and pelagic and benthic juveniles can be identified to species on the basis of characters mentioned above (Figures 2-7). In both species, transformation into the pelagic juvenile stage is initiated within the size range of 14.0 to 20.0 mm. All specimens larger than 20.0 mm have some juvenile pigmentation. The largest pelagic juvenile of *S. alascanus* encountered was 27.2 mm, whereas the smallest benthic juvenile was 22.5 mm. In contrast, in the protracted pelagic juvenile stage of *S. altivelis*, individuals may attain 56.0 mm in length. The smallest benthic juvenile of this species in the collection was 42.0 mm. Pelagic juveniles of *S. macrochir* are similar in shape and pigmentation to those of *S. altivelis*. Although the largest pelagic specimen available was only 30 mm long, it is probable that pelagic juveniles of *S. macrochir* grow larger than this and have a protracted mid-water life as in *S. altivelis*.

Relative body depth (maximum body depth/standard length) changes markedly during development and is an important taxonomic character in the pelagic juveniles (Figure 8). It is 15% at the beginning of the larval period, almost doubles by the onset of notochord flexion, and averages 28% during flexion. It increases further to 35% in larvae 7.5 to 10.0 mm. Relative body depth remains at about this percentage in larvae and pelagic juveniles of *S. alascanus* but decreases sharply to an average of 25% (range of 22 to 32%) in benthic juveniles. Late-stage larvae and pelagic juveniles of *S. altivelis* are much more robust and deeper bodied, averaging 41% (range of 36 to 45%) in the 10- to 40-mm size range. Pelagic juveniles 40 to 50 mm long begin to show a decrease in body depth (mean 38%; range of 36 to 41%), 50- to 55-mm specimens show a further decrease (mean 35%; range of 34 to 37%) and the decrease is precipitous in benthic juveniles (mean 28%; range of 27 to 30%). Body depth in 21- to 30-mm pelagic juveniles of *S. macrochir* averaged 37.5% of the body length (range of 34 to 42%).

The gut has an unusual shape in early larvae up to about 5.5 mm. The narrow, dorsally positioned esophagus runs posteriad from the head for some distance before entering the principal mass of the gut. The effect of this is to produce a space between

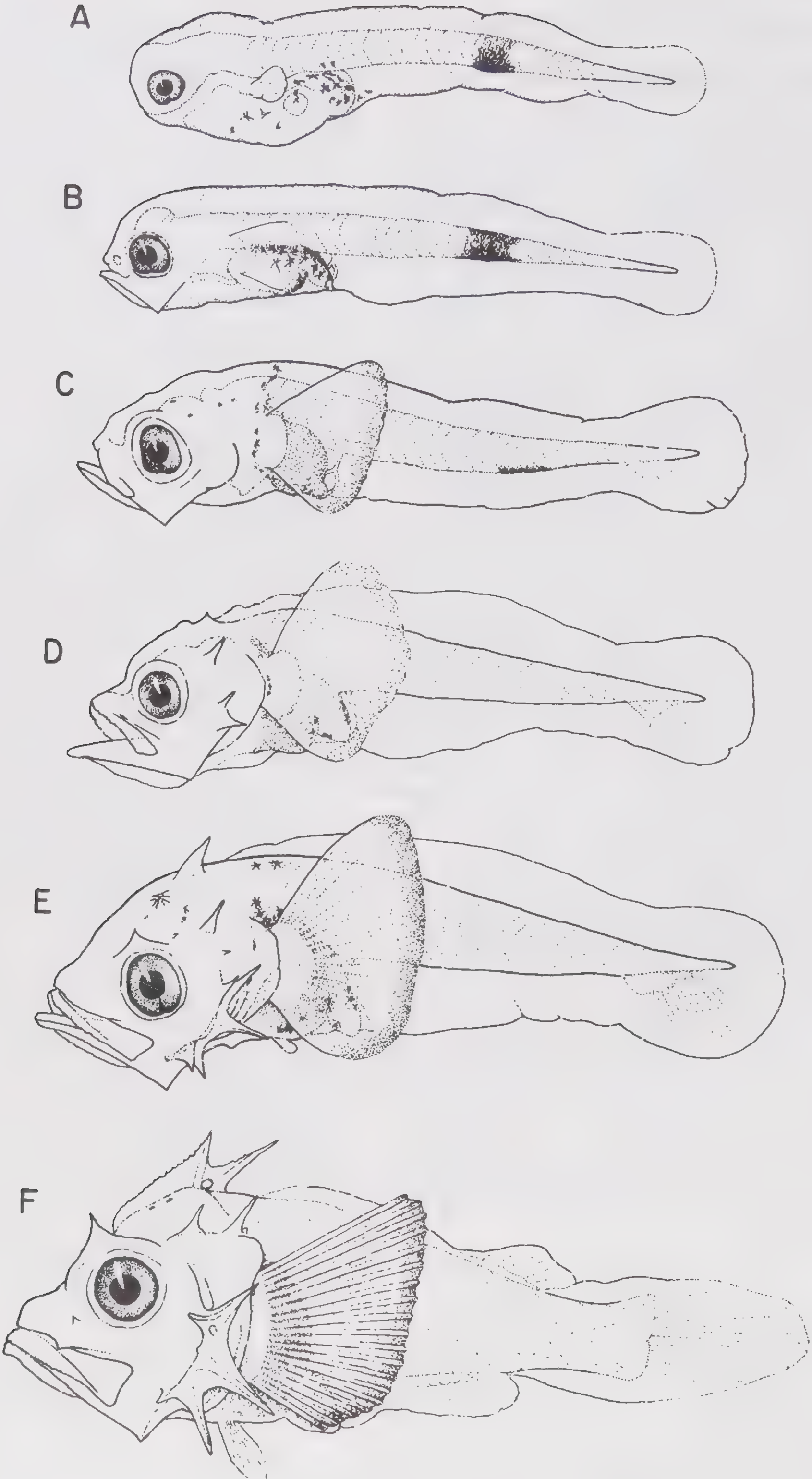

FIGURE 1.—Larvae of *Sebastolobus* spp. from CalCOFI plankton samples. A. 3.0 mm; B. 3.5 mm; C. 5.2 mm; D. 5.7 mm; E. 6.2 mm; F. 7.7 mm.

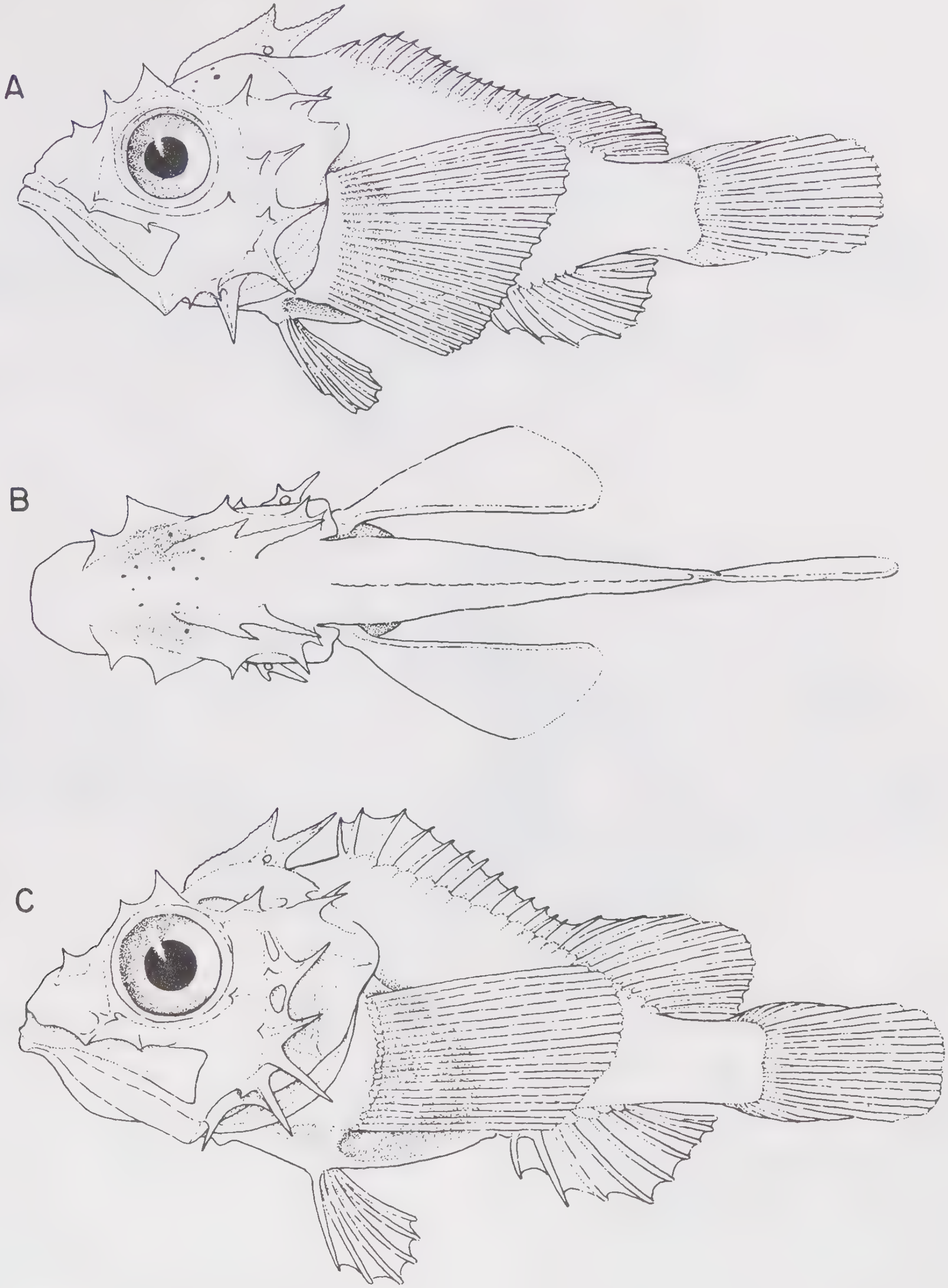

FIGURE 2.—Larvae of *Sebastolobus altivelis* from CalCOFI plankton samples. A. 11.2 mm; B. 11.2 mm, dorsal view; C. 15.4 mm.

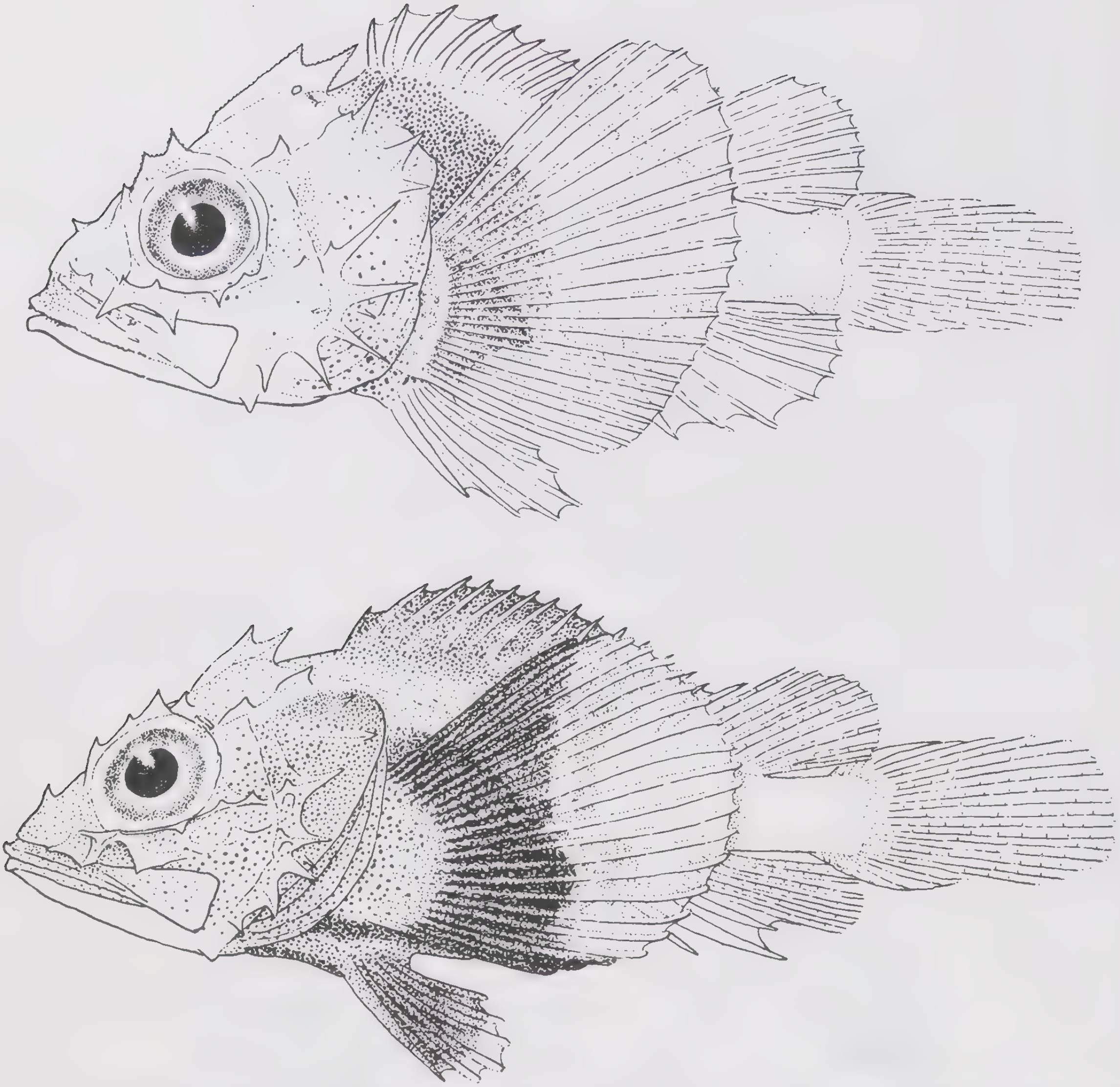

FIGURE 3.—Developmental stages of *Sebastolobus altivelis* from mid-water trawl samples. Above, 16.3-mm transforming specimen. Below, 26.8-mm pelagic juvenile.

the head and the gut (Figure 1B). The space gradually diminishes as the gut enlarges and is absent in larvae larger than 6.0 mm. Relative gut length increases markedly during development. Snout-anus distance averages 41% of the body length up to the stage of notochord flexion, 46% during flexion, and 56% in post-flexion larvae up to 10 mm in length. In larvae and transforming specimens of 10- to 20-mm *S. altivelis* there is an increase to a mean of 64% and in 20- to 56-mm pelagic juveniles there is a further increase to a mean of 68%. In early benthic juveniles snout-anus length averages 64% of body length. The gut is slightly shorter in *S. alascanus;* snout-anus length averages 61% of body length for the larvae and for the pelagic and early benthic juveniles.

The head is moderate in size in early larval stages but enlarges markedly with development. Head length increases from 23% of body length at hatching to an average of 31% during notochord flexion and is 37% in 7.5- to 10.0-mm larvae. Relative head length in larvae and pelagic juveniles of *S. altivelis* in the 10.0- to 40.0-mm size range averages 41%. A slight decrease to a mean of 39%

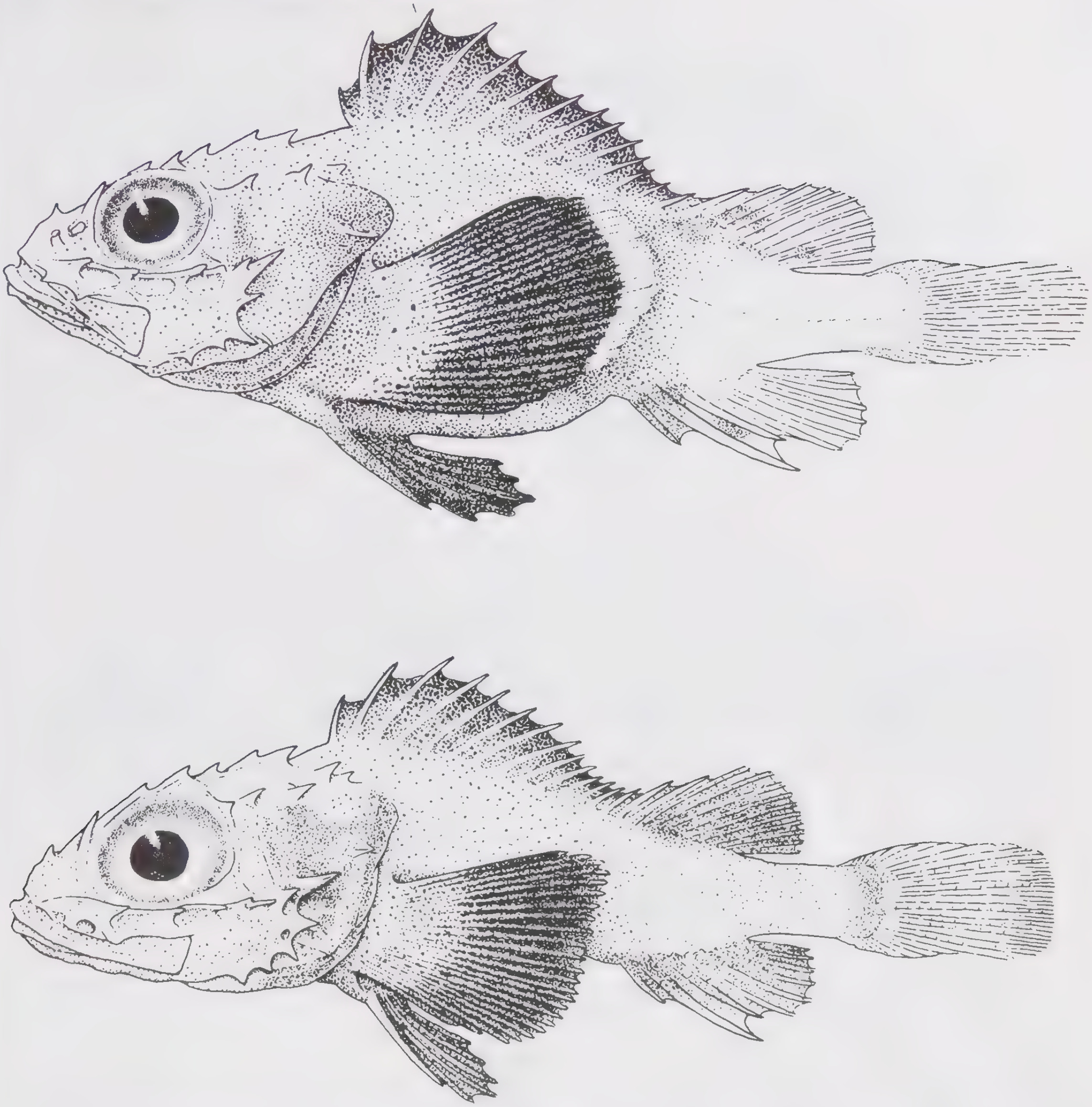

FIGURE 4.—Developmental stages of *Sebastolobus altivelis*. Above, 53.5-mm late pelagic juvenile from mid-water trawl. Below, 53.0-mm benthic juvenile from bottom trawl.

occurs in 40.0- to 56.0-mm specimens and early benthic juveniles average 38%. Virtually the same changes in relative head size occur in *S. alascanus*.

The eyes of early-stage *Sebastolobus* larvae are relatively smaller than in *Sebastes* larvae of comparable size. Eye diameter averages 26% of the head length for larvae up to the beginning of notochord flexion, 27% during flexion, and 28% in post-flexion larvae up to 10.0 mm in length. *Sebastes* larvae average 33 to 35% during comparable stages. Eye diameter in larvae and pelagic juveniles of *S. altivelis* 10.0- to 56.0-mm range) averages 31% of the head length, while in those of *S. alascanus,* eye diameter is slightly larger (mean 33%). In early benthic juveniles of both species, relative eye diameter increases sharply to a mean of 38% of head length. The snout is relatively short in pre-flexion larvae of *Sebastolobus* where snout length averages 27% of head length.

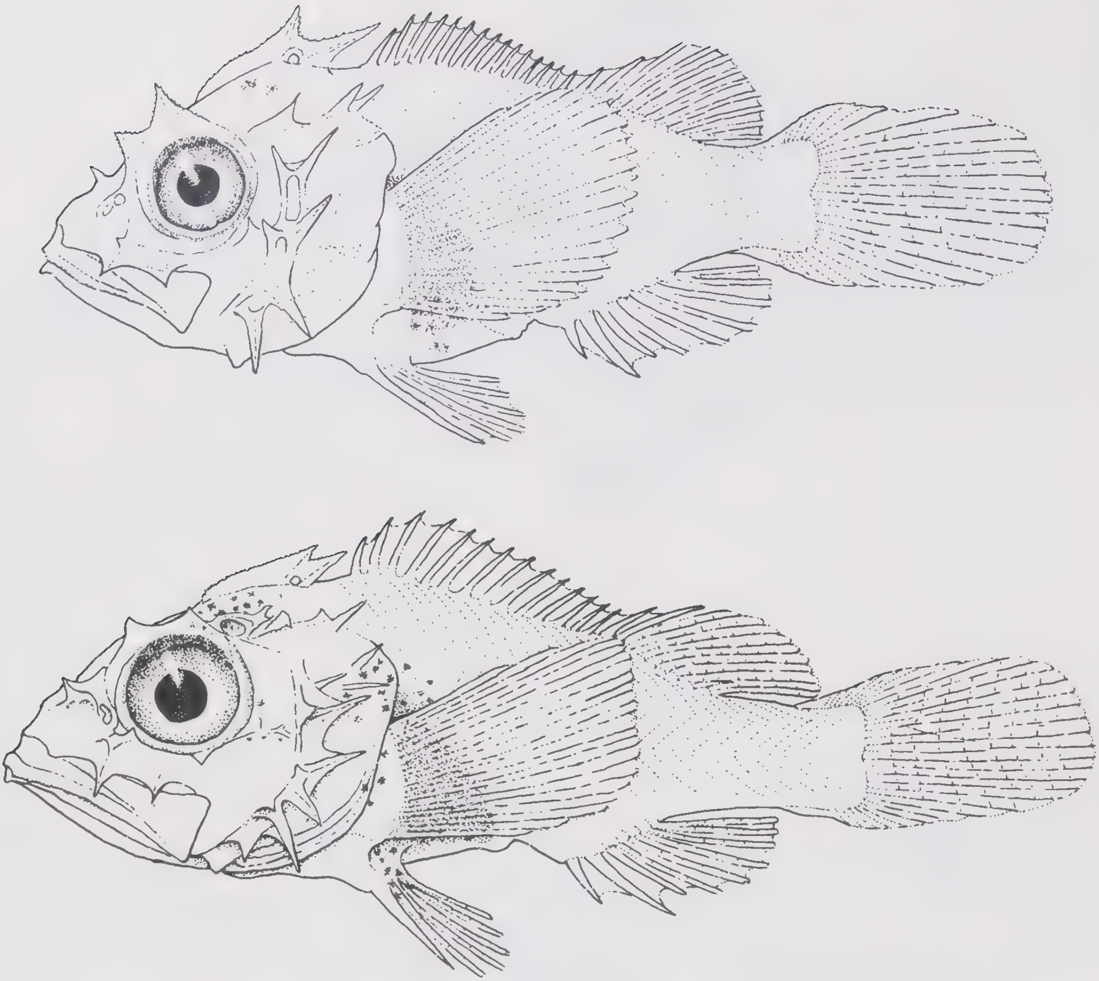

FIGURE 5.—Developmental stages of *Sebastolobus alascanus*. Above, 10.3-mm larva from mid-water trawl. Below, 16.0-mm transforming specimen from mid-water trawl.

This increases to an average 36% in 6.0- to 10.0-mm larvae. Later stages of *S. altivelis* average 28%. *Sebastolobus alascanus* in the 10.0- to 20.0-mm range average 31%, but this is reduced to 27% in the remaining stages.

Fin Development

The pectoral fins of *Sebastolobus* are undifferentiated buds in newly hatched larvae, however, when the larvae reach a length of 3.0 mm the base and blade portions of each fin are beginning to differentiate. From this stage until the initiation of notochord flexion at 6.0 mm the rayed portion of the fin enlarges rapidly to form the large fan-shaped structure characteristic of *Sebastolobus*. At this stage the fin length is about 17% of the body length. This increases to an average of 22% during notochord flexion and 27% in post-flexion larvae up to 10 mm length.

In specimens larger than 10 mm the relative length of the pectoral fin differs considerably between *S. altivelis* and *S. alascanus* (Figure 9). In specimens of *S. altivelis* in the 10- to 20-mm size range, the pectoral fin length averages 34% of the body length (range of 29 to 39%). The pectorals reach their maximum relative length in 20- to 40-mm pelagic juveniles where they average 39% of the body length (range of 35 to 41%). In pelagic juveniles 40 to 50 mm long the average is 35% (range of 32 to 37%), and the fins are still shorter in early benthic juveniles 42 to 60 mm long where they average 29% of the body length (range of 25

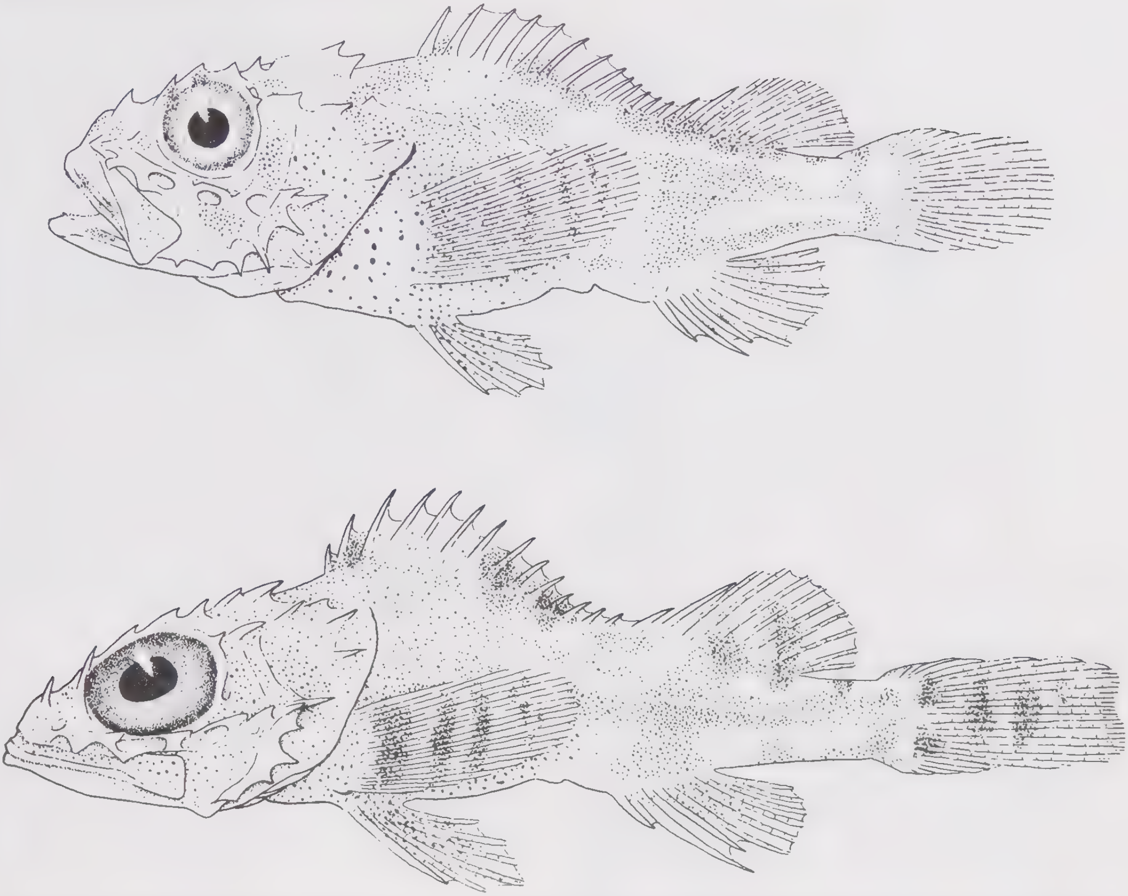

FIGURE 6.—Juveniles of *Sebastolobus alascanus*. Above, 25.3-mm newly transformed benthic juvenile from bottom trawl. Below, 50.3-mm benthic juvenile from bottom trawl.

to 33%). The pectoral fins of *S. alascanus* are considerably shorter than those of *S. altivelis* at comparative sizes. In specimens 10 to 20 mm long fin length averages 29% of body length (range of 26 to 31%). In 10- to 27-mm pelagic specimens pectoral fin length averages 29% of the body length (range of 26 to 32%). In early benthic juveniles 22 to 60 mm long, fin length is reduced to an average of 24% (range of 23 to 28%). The pectoral fin in pelagic juveniles of *S. macrochir* is even longer than in *S. altivelis*. In 21- to 30-mm specimens fin length averaged 43% of the body length (range of 40 to 44%).

The depth of the pectoral fin base is a particularly useful character in distinguishing the larvae of *Sebastolobus* from those of *Sebastes* and is also useful in separating the two species of *Sebastolobus* (Figure 10). In larvae of *Sebastes* examined (e.g., *S. paucispinis*) the depth of the fin base is about 9 or 10% of the body length through notochord flexion; thereafter it gradually diminishes, relative to body length, to about 5 or 6% in the smallest pelagic juveniles. In *Sebastolobus* there is an opposite trend of relative increase from an average of 11% (range of 10 to 15%) in pre-flexion larvae, to 18% (range of 15 to 20%) in subsequent stages of *S. altivelis* up to about 40 mm in length. In larger pelagic juveniles of *S. altivelis* the depth of the pectoral fin base begins to decrease in relation to body length. In 40- to 50-mm specimens the average is 16.5% (range of 15 to 18%) and in 50- to 56-mm pelagic juveniles it is 15% (range of 15 to 16%). It is further reduced to 14% (range of 13 to 15%) in 42- to 60-mm benthic juveniles. The pectoral fin base in *S. alascanus* is significantly shallower

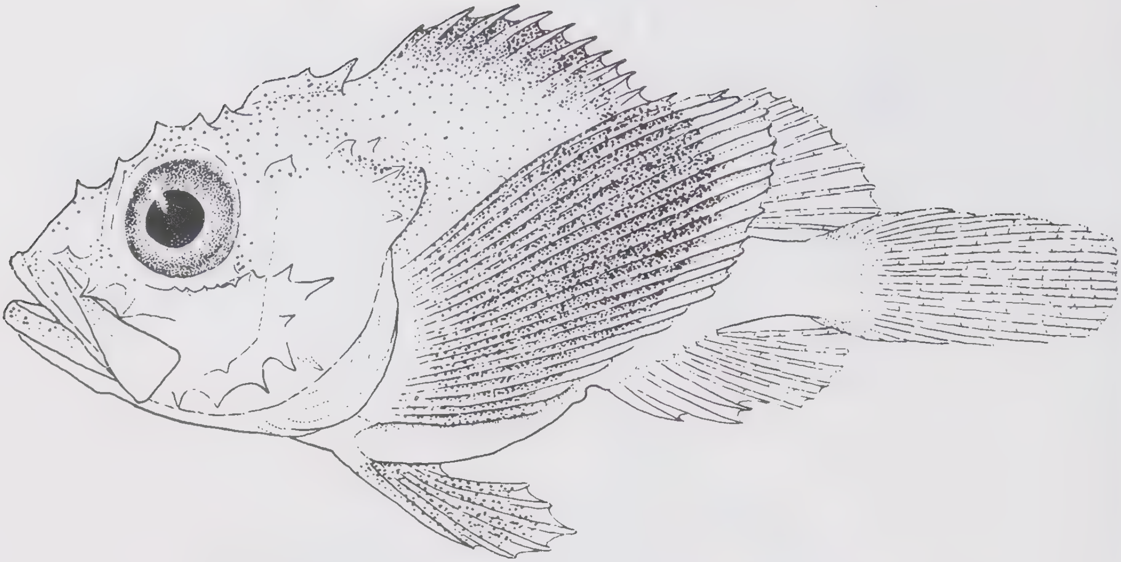

FIGURE 7.—Pelagic juvenile of *Sebastolobus macrochir* from off Kamchatka (27.2 mm).

than in *S. altivelis*. In *S. alascanus* larvae and pelagic juveniles 10 to 30 mm long the fin depth averages 14% of the body length (range of 12 to 16%). In 22- to 60-mm benthic juveniles this is reduced to an average of 10% (range of 9 to 11%).

Ossification of the pectoral fin rays begins in 6.0-mm larvae of *Sebastolobus* (Table 5). The full complements of pectoral rays, 23 to 24 for *S. altivelis* and 21 to 22 for *S. alascanus,* are present in 7-mm larvae (Tables 5, 6).

The pelvic fin buds appear in larvae of about 6.0 mm and elongate to about 12% of the body length by the completion of notochord flexion. Fin length increases to about 17 to 18% of the body length in post-flexion larvae up to 10 mm in length. In *S. altivelis* this increases further to about 24% in pelagic juveniles 20 mm long, and averages 24% (range of 21 to 27%) for the remainder of the pelagic phase. There is a slight decrease to 22% (range of 21 to 24%) in benthic juveniles up to 60 mm long. The pelvic fin is slightly shorter in *S. alascanus* averaging 19% (range of 18 to 20%) in 10- to 20-mm specimens, and 21% (range of 18 to 33%) in larger pelagic juveniles and in benthic juveniles up to 60 mm long. The full complements of one spinous ray and five soft rays are beginning to ossify in 7-mm larvae of *S. altivelis* and *S. alascanus.*

The hypural thickening of the caudal fin first appears in larvae about 3.5 mm long. The hypurals begin to ossify in 7-mm larvae of both species and the full complements of two superior and two inferior elements are ossified in 12-mm larvae of both species. The full complements of eight superior and seven inferior principal caudal rays are beginning to ossify in 7-mm larvae of *Sebastolobus.* The procurrent caudal rays also begin to ossify in 7-mm larvae. The full complements of 6

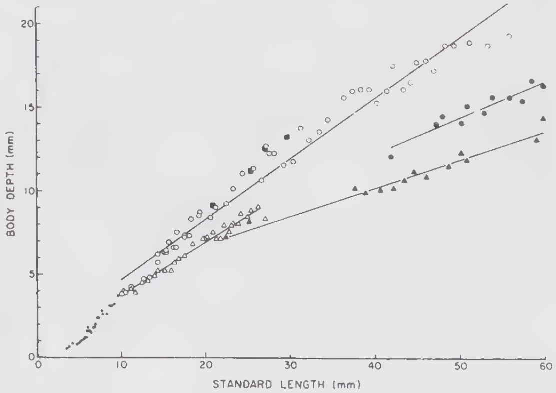

FIGURE 8.—Relationship of body depth to body length in developmental stages of *Sebastolobus*. Small dots = larvae less than 10 mm not identifiable to species. Large open circles = larvae and pelagic juveniles of *S. altivelis*. Large dots = benthic specimens of *S. altivelis*. Open triangles = larvae and pelagic juveniles of *S. alascanus*. Solid triangles = benthic specimens of *S. alascanus*. Solid squares = pelagic specimens of *S. macrochir*. Lines fitted by method of least squares. No regression line drawn for *S. macrochir*.

to 9 superior and 7 to 9 inferior procurrent rays are present in 10-mm larvae of *S. altivelis* and the full complements of 8 to 10 superior and inferior elements are present in 12- to 13-mm larvae of *S. alascanus*.

The dorsal and anal fins begin to develop in 6-mm larvae of *Sebastolobus* and the full complements of rays are ossifying in 7-mm larvae of both species. In *S. altivelis* the usual number of spinous dorsal rays is 15 and in *S. alascanus* the usual number is 16. Both species have 8 to 10 soft dorsal rays with a usual number of 9.

Pigmentation

The melanophore pattern of embryos and yolk-sac larvae of *Sebastolobus* has been described by Pearcy (1962). At the beginning of the larval stage (3.5 mm) the melanophore pattern is distinctive. Large median melanistic blotches oppose each other about midway back on the tail (Figure 1A, B). In some specimens, the blotches are expanded to form a band. Also, melanophores cover the dorsolateral surfaces of the posterior region of the gut. The melanistic tail blotches are transitory; they are lost in some larvae as small as 4.2 mm and one or both are absent in most larvae between 5.0 and 6.0 mm in length. The dorsal spot was absent in all larvae larger than 6.0 mm and the ventral spot was absent in all larger than 6.4 mm. In contrast, the gut pigment is augmented throughout the larval period, extending forward to the axillary region and internally anterior to the cleithrum in larvae about 5.0 mm long. When the larvae reach 6.0 mm the pigment extends onto the ventral surface of the gut and dorsally as deeply embedded pigment at the nape. With continued development the melanophores form a solid sheath on the peritoneum surrounding the gut.

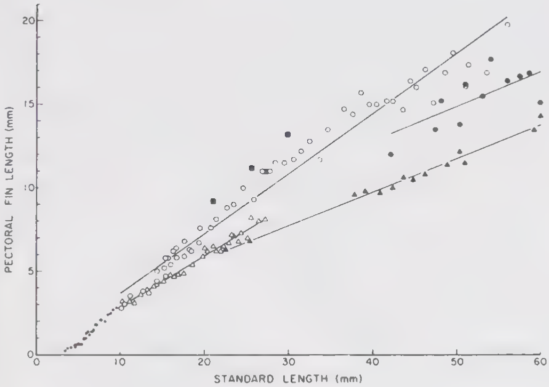

FIGURE 9.—Relationship of pectoral fin length to body length in *Sebastolobus*. Symbols as in Figure 8.

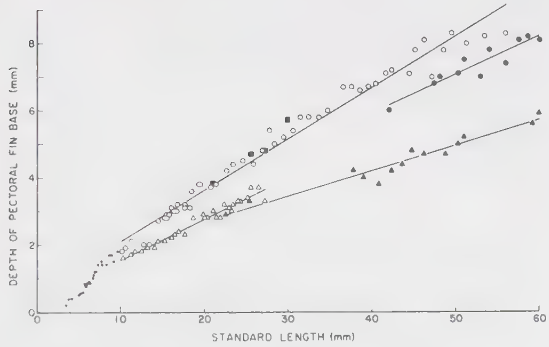

FIGURE 10.—Relationship of depth of pectoral fin base to body length in *Sebastolobus*. Symbols as in Figure 8.

Melanophores appear at the posterior margin of each pectoral fin in some larvae as small as 4.0 mm. About half the larvae examined between 4.0 and 5.0 mm have this posterior margin of fine melanophores and the pigment is present in all larvae in the 5.0- to 11.0-mm range. The melanophores are then lost, and almost all larvae larger than 11.0 mm have pigmentless fins.

Melanophores appear on the posterior lobes of the brain in 5.2- to 7.0-mm larvae and are present in all larvae larger than this. They also appear above the anterior lobes of the brain in larvae between 7.0 and 9.0 mm in length and in most larvae larger than 9.0 mm.

Juvenile pigmentation begins to appear in some specimens of *S. altivelis* of the 14- to 20-mm size range. On the head, patches of melanophores appear on the opercle, cheek, snout, and jaws. In most specimens larger than 22 mm, the patches are confluent, and the head is generally dusky with darker areas at the opercle and along the upper jaw.

A patch of melanophores appears superficially over each side of the gut in specimens as small as 14 mm. These patches expand to form a solid melanistic sheath in some specimens of the 14- to 20-mm size range. The posterior margin of the sheath is an arc running from the vent to the nape and stands out sharply against the pigmentless region of the trunk posterior to the sheath. With continued development the pigment sheath expands posteriad and is a striking feature of the pelagic juveniles. In the 20- to 30-mm size range the sheath extends posteriad to a vertical from the first or second anal fin spines. In the 30- to 40-mm size range the sheath extends posteriad to the 2nd or 3rd anal spine in most specimens and to the soft dorsal fin in some. In most pelagic juveniles of the 40- to 50-mm size range the dusky sheath extends back to the soft dorsal and it does so in all specimens of the 50- to 60-mm size range. When the juveniles become benthic, the dusky sheath extends posteriad to the caudal fin.

The fins become deeply and characteristically pigmented in juveniles of *S. altivelis*. The anterior portion of the spinous dorsal fin becomes melanistic in specimens as small as 18 mm. In juveniles of the 20- to 25-mm size range the anterior one-half to two-thirds of the fin is melanistic. In the 25- to 30-mm range three-fourths or more of the fin is black. In pelagic juveniles larger than this the pigment has spread onto the soft dorsal fin, and covers both the soft dorsal and soft anal fins in benthic juveniles.

The bases of the pectoral fins begin to be covered with melanophores in specimens as small as 14 mm. In specimens as small as 18 mm the melanophores extend onto the basal region of the rays. With further growth this black basal zone enlarges posteriad and becomes a highly characteristic feature of the pelagic juveniles. The posterior margin of this zone contrasts sharply with the distal clear region of the fin. In juveniles of the 19- to 25-mm size range the width of the black basal zone averaged 20% of the fin length. Enlargement of this zone is shown by the average relative widths for successive size ranges (25 to 30 mm, 38%; 30 to 35 mm, 46%; 35 to 40 mm, 54%; 40 to 45 mm, 65%; 45 to 50 mm, 72%; 50 to 55 mm, 76%). Towards the end of the pelagic juvenile stage a pale translucent layer covers the basal region of the pectoral fin and thus gives the black zone the appearance of a band. The huge pectoral fins, each with their broad black band, are distinctive features of the pelagic juveniles of *S. altivelis*. When the juveniles become benthic the black zone extends to the tips of the fins. Like the pectoral fins, the pelvic fins also develop a black-pigment zone that enlarges with development. In 20- to 25-mm juveniles the basal one-quarter to three-quarters of each fin may be black, although in the majority of specimens the basal one-half is black. In the 25- to 30-mm range most specimens have three-fourths or more of the fin black and in juveniles larger than 30 mm either the fin is entirely black or the extreme tips of the rays are pigmentless.

Juvenile pigment begins to appear in *S. alascanus* in the 14- to 20-mm size range. The first head pigment to appear is a melanistic blotch on the posterior region of the opercle. This gradually spreads anteriorly onto the cheek and in late-stage pelagic juveniles the entire head is speckled with melanophores. A blotch begins to form over each side of the gut in larvae as small as 15 mm. These enlarge dorsad onto the spinous dorsal fin and posteriad as an irregular mottled sheath that contrasts markedly with the solidly pigmented sheath of *S. altivelis* juveniles. In the largest pelagic juveniles the mottling on the dorsal fin and trunk extends posteriad to a vertical from the vent. When the juveniles become benthic the mottling spreads onto the remainder of the body and median fins. Melanophores appear on the bases of the pectoral fins in specimens of the 14- to 20-mm size range. A faint band of melanophores appears on the rays in some specimens of this size range but never becomes highly developed and covers only the basal one-third of the fin in the largest pelagic juveniles. Likewise a faint band of pigment develops on each pelvic fin in specimens as small as 16 mm and only covers the basal half of the fin in the largest pelagic juveniles. When the juveniles become benthic the pectoral fins develop a pattern of four narrow irregular bands.

DISTRIBUTION

The genus *Sebastolobus* has an exceptionally wide latitudinal distribution in the eastern Pacific. *Sebastolobus altivelis* ranges from the Aleutian Islands southward to Cape San Lucas, Baja California, and *S. alascanus* inhabits waters from the Bering Sea to northern Baja California (Barsukov, 1964; Miller and Lea, 1972). The extensive north-south range of *Sebastolobus* is probably related to habitat depth rather than eurythermy. They are deep-living species throughout their latitudinal range and, as such, experience little change in habitat temperature towards the southern end of their range. Alverson et al. (1964) reported that significant catches of *Sebastolobus* are taken at depths shallower than 150 fathoms in the trawl fishery from Oregon to southeastern Alaska, but that the percentage contribution of *Sebastolobus* increased with depth. At the maximum depth range sampled, 500 to 600 fathoms, *Sebastolobus* accounted for about 70% of the total fish catch. Southward of Oregon the shoaler elements of the *Sebastolobus* populations are gradually eliminated and, off southern California, adults of even the shallower-living species, *S. alascanus,* are generally restricted to waters deeper than 150 fathoms.

Curtailment of spawning or mortality of fertilized eggs off southern California is evident from the distribution of *Sebastolobus* larvae in the CalCOFI sampling area (Figures 11, 12). In 1966, there were no occurrences south of line 97, which runs seaward from the Mexican border, and in 1969 *Sebastolobus* occurred on only two stations below this line. It is apparent that the CalCOFI sampling pattern did not encompass the offshore limits of larval distribution and that larvae occur well seaward of the 200 to 250 mile coastal zone sampled during these years.

The seasonal abundance of *Sebastolobus* larvae for 1966 and 1969 is shown in Table 7. In 1966 larvae were taken from April to October in central and southern California. Numbers of larvae and occurrences were highest in April and diminished in subsequent months. No larvae were taken south of southern California in 1966. In 1969, larvae appeared earlier in the year, from January to December off central California, from January to October off southern California, and from June to September off northern Baja California. Again, numbers of larvae and occurrences peaked in April off central and southern California. Data for the two species are lumped together in Table 7. Of the larvae identifiable to species, those over 10 mm, 6% were *S. alascanus* in 1966 and 12% were *S. alascanus* in 1969. Thus, the data in Table 7 pertain largely to *S. altivelis.*

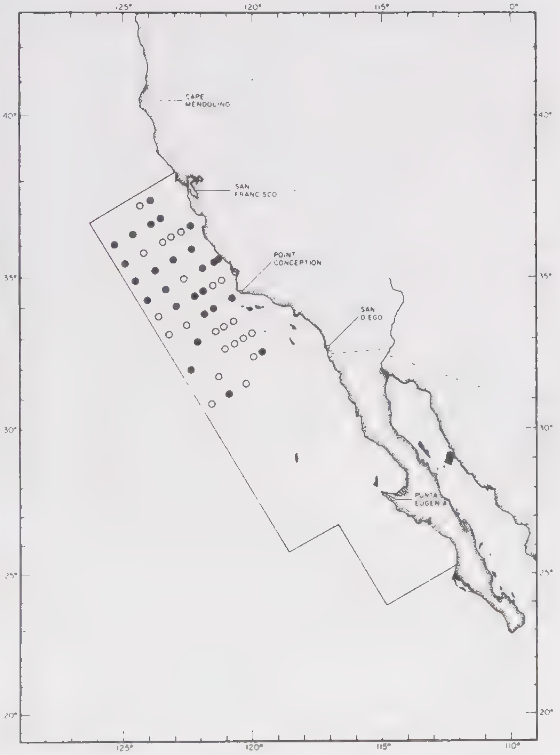

FIGURE 11.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1966. Dots indicate stations where numbers of *Sebastolobus* larvae exceeded mean number (7.2) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

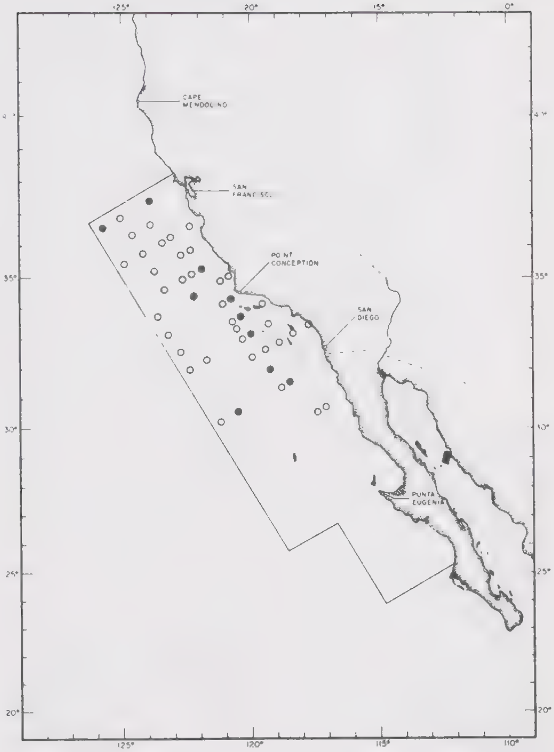

FIGURE 12.—Stations at which larvae of *Sebastolobus* were collected during CalCOFI survey of 1969. Symbols as in Figure 11.

Although *Sebastolobus* larvae are taken in plankton tows over a large proportion of the year, the spawning season is relatively short. Table 8 shows the seasonal change in the size of *Sebastolobus* larvae. The mean size increases steadily throughout the year and small, recently spawned larvae, less than 5 mm, do not occur after June in 1966 and May in 1969. This indicates a spawning season of 4 or 5 mo.

Information on the growth rate of the pelagic juveniles of both species of *Sebastolobus* was obtained by examining mid-water trawl samples

TABLE 7.—Standard numbers and occurrences of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations. Dashes indicate region not occupied.

		Month																				
		Jan.		Feb.		Apr.		May		Jun.		Jul.		Aug.		Sep.		Oct.		Nov.		Dec.	
	Year	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.
Central California CalCOFI Lines 60-77	1966	-	-	0	0	227	19	0	0	89	14	67	10	0	0	0	0	13	3	-	-	-	-
	1969	3	1	12	4	81	10	10	2	0	0	17	5	38	9	0	0	14	4	-	-	3	1
Southern California CalCOFI Lines 80-93	1966	-	-	-	-	58	10	34	7	3	1	10	3	37	4	39	8	17	3	-	-	-	-
	1969	3	1	3	1	-	-	3	1	0	0	19	6	13	4	-	-	3	1	-	-	-	-
Northern Baja California CalCOFI Lines 97-107	1966	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1969	-	-	-	-	-	-	0	0	10	2	13	3	0	0	6	2	-	-	-	-	-	-

from the Los Angeles County Museum, Scripps Institution of Oceanography, and the Southwest Fisheries Center. A total of 260 samples from the years 1950 to 1969 were examined. Most of the samples were taken in the deepwater basins off southern California, but two samples of *S. alascanus* were taken as far north as Crescent City, Calif., and one sample of *S. altivelis* was from the vicinity of Guadalupe Island, Baja California.

The composite monthly size frequencies of mid-water trawl specimens of *S. altivelis* are shown in Figure 13. Two major size classes are present from May through September. One class is formed by larvae and transforming specimens, less than 20 mm in length, from the January-May spawning season. The other class is formed

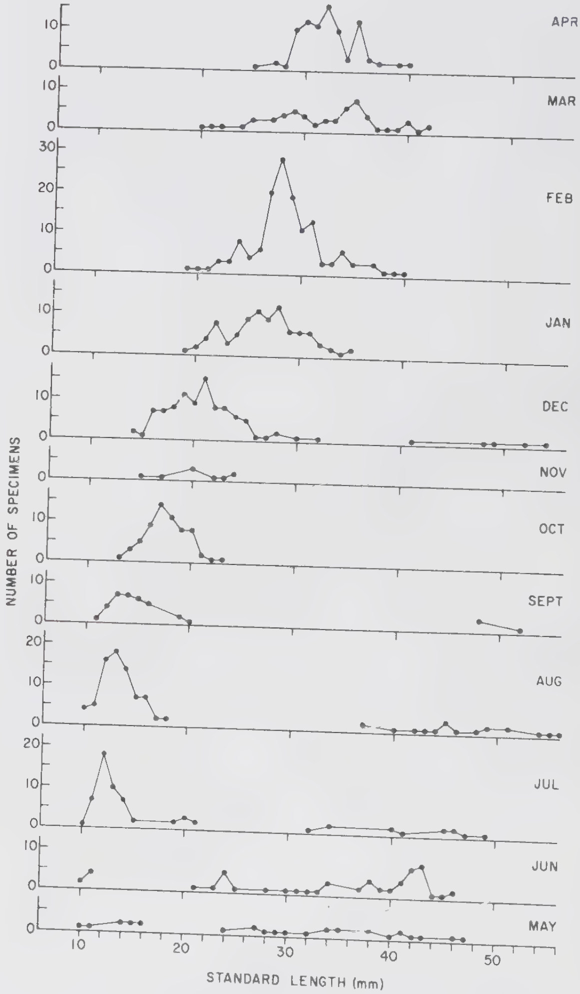

FIGURE 13.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus altivelis* from mid-water trawls.

Table 8.—Mean lengths with standard deviations in mm (A) and size ranges in mm (B) of *Sebastolobus* larvae taken during 2 yr of the California Cooperative Oceanic Fisheries Investigations.

Year	Month									
	Jan.		Feb.		Apr.		May		Jun.	
	A	B	A	B	A	B	A	B	A	B
1966	-	-	-	-	4.3 ± 1.07	2.2 - 6.9	6.2 ± 1.16	4.2 - 7.8	7.4 ± 1.17	5.1 - 10.0
1969	3.1 ± 0.65	2.8 - 3.4	3.0 ± 0.47	2.8 - 3.4	3.6 ± 0.76	2.6 - 4.7	4.2 ± 0.98	3.1 - 5.2	8.6 ± 0.68	8.1 - 8.9

Year	Month									
	Jul.		Aug.		Sep.		Oct.		Dec.	
	A	B	A	B	A	B	A	B	A	B
1966	8.7 ± 1.15	6.2 - 11.2	11.6 ± 1.42	9.2 - 15.2	14.0 ± 1.57	9.2 - 17.7	16.4 ± 1.37	14.4 - 19.3	-	-
1969	10.8 ± 1.15	8.9 - 13.2	11.8 ± 1.58	9.2 - 18.2	17.0 ± 1.10	16.2 - 17.9	16.3 ± 1.43	15.2 - 18.6	15.0	15.0

by large pelagic juveniles from the previous year's spawning season. A single size class of transforming specimens is present in October and November, however, the absence of the large pelagic juveniles is probably due to inadequate sampling, since they are present in December. From January through April a single class of pelagic juveniles is present. In summary, the early life history of *S. altivelis* is as follows: larvae are produced in a 4- or 5-mo spawning season that peaks in April. Transformation into pelagic juveniles begins as early as July and by the end of December most have completed transformation. The prolonged pelagic juvenile stage lasts until the following summer when the juveniles begin to settle to the bottom. This process probably extends over a 6- to 8-mo period with some juveniles remaining pelagic until December. The total period spent in the pelagic environment from spawning to settling is about 20 mo. The means of the composite monthly length frequencies are plotted in Figure 14 to give an estimation of growth of this species.

The composite monthly length frequencies for mid-water trawl-caught specimens of *S. alascanus* are shown in Figure 15. In contrast to *S. altivelis,* only a single size class is present each month. From July to December a single class of larval and transitional specimens less than 20 mm long is present. Some pelagic juveniles are present in December and by January most of the specimens have completed transformation. Successive samples from February to May contain only pelagic juveniles. In summary, the planktonic and early pelagic life history of *S. alascanus* is similar to that of *S. altivelis*. A probable 4- or 5-mo spawning period that peaks in April gives rise to larvae that appear in mid-water trawl samples in summer. Transformation into the pelagic juveniles begins as early as August and most have completed transformation by the end of December. A class of pelagic juveniles is present from December through May, however, the size ranges for these months overlap the range at which *S. alascanus* juveniles begin to settle to the bottom, and it is

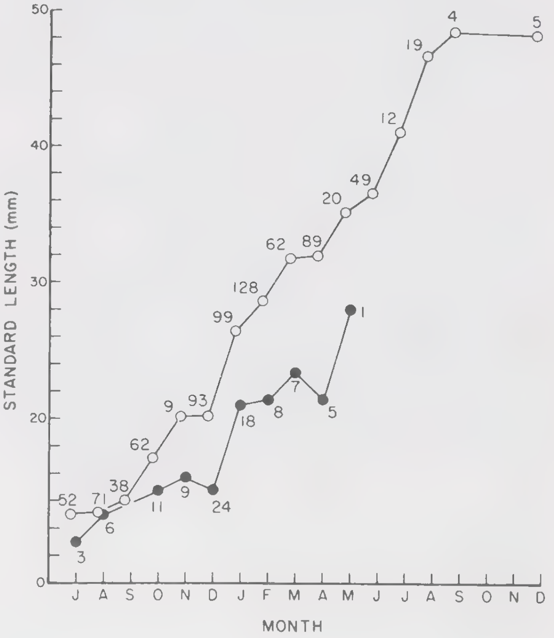

FIGURE 14.—Means of composite monthly size frequencies of larvae and pelagic juveniles of *Sebastolobus altivelis* and *S. alascanus* from mid-water trawls.

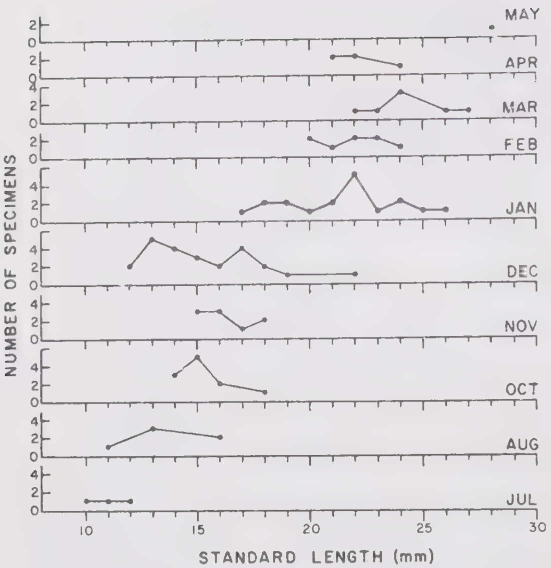

FIGURE 15.—Composite monthly size frequencies for larvae and pelagic juveniles of *Sebastolobus alascanus* from mid-water trawls.

probable that settling begins as early as January. Most have become benthic by May or June. The pelagic juvenile stage in this species is short-lived compared with *S. altivelis* and the total period spent in the pelagic environment from spawning to settling is about 14 or 15 mo. The means of the composite monthly frequencies are plotted in Figure 14.

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ROLE OF LARVAL STAGES IN SYSTEMATIC INVESTIGATIONS OF MARINE TELEOSTS: THE MYCTOPHIDAE, A CASE STUDY[1]

H. Geoffrey Moser and Elbert H. Ahlstrom[2]

ABSTRACT

The lanternfish family Myctophidae is the most speciose and widespread family of mid–water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

Our studies of myctophid larvae, on a worldwide basis, have demonstrated that characters of the larval stages of lanternfishes are of great utility in systematic analysis. The genera and species can be recognized on the basis of eye and body shape, the shape and length of the gut, and pigment pattern and by the sequence of photophore development. In this paper the larvae of 55 species representing 24 genera are illustrated and used to demonstrate the usefulness of larvae in understanding the relationships of species within genera.

Characters of the larvae provide insight into generic affinities of lanternfish, allowing us to construct an evolutionary scheme of tribes and subfamilies that differs in some aspects from those proposed on the basis of adult characters. The concept of using larval characters in combination with adult characters to delineate phylogenetic lines in myctophids is discussed, as is our view of evolutionary strategy in the family.

A major facet of comprehensive systematic investigations is the search for functionally unrelated characters. Whether the independence of these characters is actual or merely apparent, they constitute useful elements in the analysis of systematic relationships. Ample evidence of this is the higher classification of teleosts (Greenwood et al., 1966) generated by the synthesis of a diverse array of classical taxonomic characters. The recent surge of serological and biochemical studies on fish has placed a fresh group of characters in the hands of systematic ichthyologists (De Ligny, 1969). Likewise, recent advances in fish cytogenetics (e.g., Ohno, 1970; Benirschke and Hsu, 1971; Ebeling, Atkin, and Setzer, 1971) are providing another group of taxonomic characters. It is likely that behavioral science will be still another source of taxonomic characters, as exemplified by the growing body of information on the acoustic behavior of fishes (Fish and Mowbray, 1970).

One group of well known taxonomic characters, those of the embryonic and larval stages, has received scant attention from all but a few systematic ichthyologists. Characters of the larvae have played a large role in the taxonomy of anguilliform fishes (Castle, 1969) partly because of the conspicuousness of eel leptocephali and partly because of the unavailability of adults of many of the families. Bertelsen's (1951) treatment of the ceratioid fishes is a superb example of the value of utilizing larval stages in a systematic revision of a large group of teleosts. Apart from these two groups, it is the larvae of myctophiform fishes which have received the most attention from taxonomists. Ege (1953, 1957) relied heavily on larval stages in his extensive works on the Paralepididae. Johnson (1971) employed larval characters in defining species and genera of Scopelarchidae. Bertelsen, Marshall, and Krefft (pers. commun.) have used larval stages extensively in their revision of the Scopelosauridae. Our studies on the family Myctophidae itself (Moser and Ahlstrom, 1970, 1972) indicated that larval characters can aid significantly in differentiating taxa and defining evolutionary lineages within this family.

The lanternfish family Myctophidae is the most speciose and widespread family of mid–water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

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Our studies of the larvae of this family have included material from all oceans. We have been able to identify larvae from all recognized genera except *Hintonia* and *Dorsadena*. Larval evidence supports giving generic status to *Metelectrona* and *Parvilux*. Including these, we have developmental series for 29 myctophid genera and for many genera we have series for all known species. This has afforded a more comprehensive view of the range and variability of larval characters, and we are increasingly impressed with the functional independence of the larval and adult characters. It is apparent that the world of the larvae and the world of the adults are two quite separate evolutionary theaters. Our studies of larval lanternfishes have disclosed a full range of characters, from generalized to specialized and from conservative to labile, equal in scope to those of the adults. These characters fall into several categories. An important group is the shape of various structures such as the eye, head, trunk, guts, and fins, especially the pectoral fins. Another group is the sequence of appearance and the position of fins, photophores, and bony elements. Another is the size of the larvae when fins and other features appear and the size of the larvae when they transform into juveniles. Pigmentation provides an important group of characters based on the position, number, and shape of melanophores. Finally, there are the highly specialized larval characters such as voluminous fin folds, elongated and modified fin rays, chin barbels, preopercular spines, etc. It is our purpose here to point out some of these characters and demonstrate how they can be of advantage in defining taxa and establishing phylogenetic lineages.

THE SUBFAMILY MYCTOPHINAE

The most trenchant character of larval myctophids is eye shape. Our studies show that lanternfish larvae fall naturally into two groups on the basis of eye shape—those with narrow elliptical eyes and those with round or nearly round eyes (Moser and Ahlstrom, 1970). The species composition of these two groups agrees closely with that of the two subfamilies, Myctophinae and Lampanyctinae, established by Paxton (1972) on the basis of osteological and photophore characters of adults. Larvae of the Myctophinae have elliptical eyes; some species have ventral prolongations of choroid tissue and some have the eyes on stalks. Paxton recognized 11 genera in the subfamily Myctophinae and distributed them into two tribes, the Myctophini and the Gonichthyini. Larvae of the species in each of these genera generally conform to a particular morph based on form, pigment, and developmental pattern and, although these morphs are remarkably diverse, we can find no character or set of characters that would divide the genera into tribes. Within each genus of the subfamily, however, the larval characters are indispensible in delineating groups of related species or subgenera. This is best illustrated by examining the important genera of the Myctophinae.

Protomyctophum larvae have a slender shape (Figure 1). For all species except *P. anderssoni,* the gut is short during most of the larval period and characteristically there is a marked interspace between the anus and the origin of the anal fin (Figure 1A-D). The gut elongates dramatically in late larvae, to fill the interspace. Gut development is completely dissimilar in *P. anderssoni,* where the gut is long at all larval sizes, in fact longer than in most other lanternfish larvae (Figure 1E). Series of ventral tail melanophores are formed in some species of both recognized subgenera (*Heirops* and *Protomyctophum* sensu stricto), for example in *P. Protomyctophum normani* (Figure 1A) and *P. Heirops thompsoni* (Moser and Ahlstrom, 1970). Larvae of the subgenera can be separated, however, on the basis of eye shape, the eyes of *Heirops* (Figure 1C, D) being characteristically narrower than those of *Protomyctophum* sensu stricto (Figure 1A, B). Choroid tissue is absent from the ventral surface of the eye in all species of the genus except *P. anderssoni,* which has a well-developed "teardrop" (Figure 1E). Larvae of *P. anderssoni* are so markedly different from those of all other species of *Protomyctophum,* which otherwise form a rather cohesive group, that this species should be placed in a separate subgenus or perhaps even in a distinct genus. This suggestion is supported by the unique placement of certain photophores and by the structure of the supracaudal luminous tissue in adults of this species.

Larvae of the genus *Electrona* are a less homogeneous group but are united by a commonality of body shape and especially gut shape (Figure 2). A marked interspace is present between the end of the gut and the origin of the anal fin. This space is closed only at the termination of the

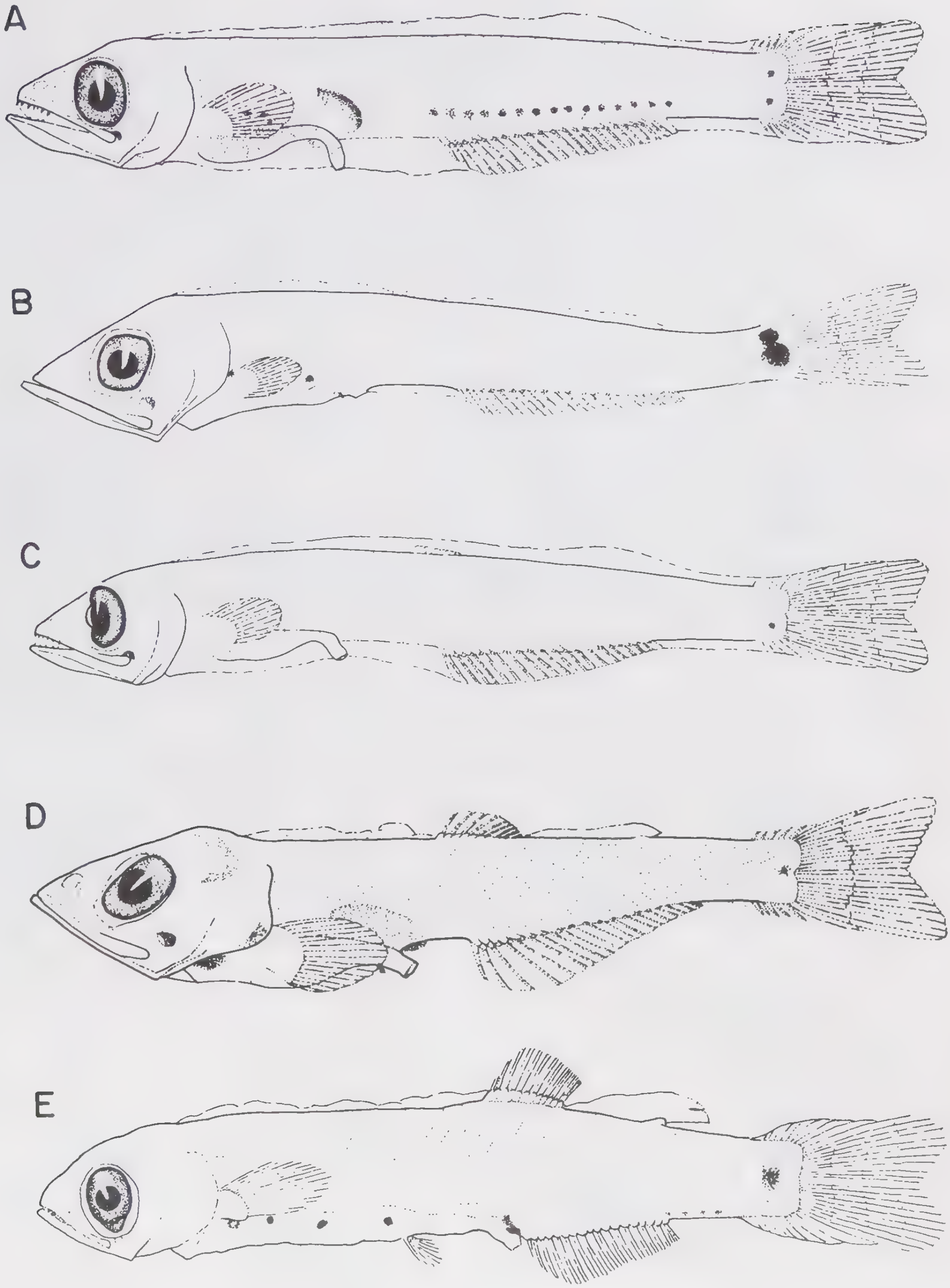

FIGURE 1.—Larvae of *Protomyctophum*. A. *P. Protomyctophum normani*, 15.2 mm; B. *P. Protomyctophum tenisoni*, 14.5 mm; C. *P. Hierops subparallelum*, 15.2 mm; D. *P. Hierops chilensis*, 11.0 mm; E. *P. anderssoni*, 15.7 mm.

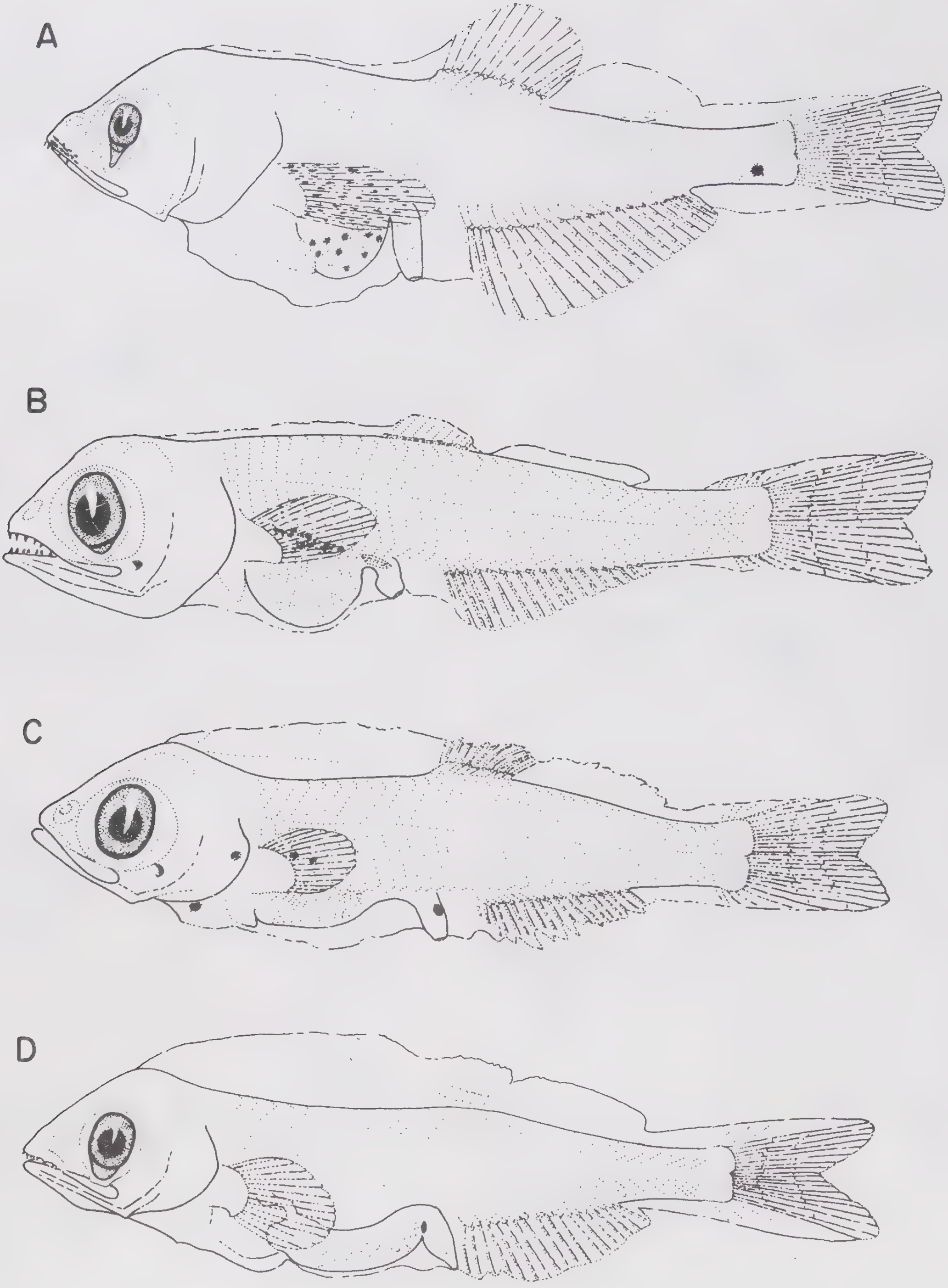

FIGURE 2.—Larvae of *Electrona* and *Metelectrona*. A. *E. antarctica*, 12.7 mm; B. *E. carlsbergi*, 11.1 mm; C. *E. subaspera*, 10.5 mm; D. *M. ahlstromi*, 10.3 mm.

larval period. None of the species forms photophores during the larval period other than the Br$_2$ pair.

The characters that most clearly separate the three developmental lines in *Electrona* are eye shape and the amount of choroid tissue developed under the eye. *Electrona antarctica* has an elongate choroid mass uniquely divided into two narrow eyes (Figure 2A). Also, *E. antarctica* larvae attain a large size (20 mm), are the deepest-bodied of all *Electrona* larvae, and have the heaviest pigmentation. The two species in the second developmental line transform at a small size (ca. 10 mm in *E. rissoi* and 12-13 mm in *E. carlsbergi*), have a small choroid mass under a moderately narrow eye, and develop scant pigment (Figure 2B). In the third line, consisting of *E. subaspera* and *E. paucirastra,* the eye is the least narrow, has no choroid tissue, and the larvae attain a large size (20 mm) (Figure 2C).

The larva of the species described as *Metelectrona ahlstromi* (Wisner, 1963) is illustrated in Figure 2D. It is more laterally compressed than any species of *Electrona* and has no interspace between the anus and origin of the anal fin. In some features it resembles the larvae of *Hygophum*; it has a late-forming dorsal fin and the gut is shaped very similarly to that in *H. taaningi* and *H. macrochir*. Its pigment is unique and the eye is distinct, with the ventral edge of the scleral envelope characteristically squared off. Also, in late-stage larvae, in addition to the Br$_2$, a second pair of photophores (PO$_5$) develops, a feature found in neither *Hygophum* nor *Electrona*. Paxton (1972) synonymized *Metelectrona* with *Electrona* and suggested that *M. ahlstromi* and *E. ventralis* are synonyms, however, the uniqueness of the larva strongly suggests the resurrection of *Metelectrona* as a valid genus.

The genus *Benthosema* is the least cohesive of any genus in the subfamily Myctophinae, from the viewpoint of larval structure (Figure 3). We can find only four types of larvae in the world ocean, although Nafpaktitis (1973) recognizes five species on adult characters. We cannot distinguish larvae of *B. pterota* and *B. panamense* although Nafpaktitis has listed a number of convincing characters that distinguish the adults of the two species. We find two highly divergent species pairs. One is composed of *B. glaciale* and *B. suborbitale* with a narrow eye subtended by a lunate choroid mass and with a pronounced interspace between the anus and the anal fin origin, reminiscent of *Protomyctophum* and *Electrona* (Figure 3A-C). In the other pair, consisting of *B. panamense-pterota* and *B. fibulatum,* the eye is wider, is subtended by a mere sliver of choroid tissue and the gut, of moderate length, lacks a postanal interspace (Figure 3D, E).

The one feature held in common by the four species is the development of some photophores in addition to the Br$_2$ during the larval period. The only other myctophine genera that develop photophores in addition to the ubiquitous Br$_2$ during the larval period are *Diogenichthys, Myctophum,* and *Metelectrona*. This feature is much more prevalent among genera of the Lampanyctinae and is helpful in defining groups of related genera there (Moser and Ahlstrom, 1972).

In *B. panamense-pterota* and *B. fibulatum* the Dn pair is formed soon after the Br$_2$ at about 5.0-6.0 mm. The PO$_5$ pair is the third to appear in

TABLE 1.—Sequence of photophore formation in larvae of three species of *Benthosema*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
B. fibulatum	ca. 4.0	Br$_2$	1	13.2
	5.4	Br$_2$ Dn	2	
	6.0	Br$_2$ Dn PO$_5$	3	
	6.4	Br$_2$ Dn PO$_5$ PO$_1$	4	
	7.3	Br$_2$ Dn PO$_5$ PO$_1$ AOa$_1$	5	
	7.7-8.7	Br$_2$ Dn PO$_5$ PO$_1$ AOa$_1$ PO$_2$	6	
	ca. 10.0	Br$_2$ Dn PO$_5$ PO$_1$ AOa$_1$ PO$_2$ Op$_2$ VLO	8	
B. pterota (panamense)	4.0	Br$_2$	1	11.8
	5.0	Br$_2$ Dn	2	
	6.0	Br$_2$ Dn PO$_5$	3	
	ca. 7.0	Br$_2$ Dn PO$_5$ PVO$_1$	4	
	7.1	Br$_2$ Dn PO$_5$ PVO$_1$ Op$_2$	5	
	7.5	Br$_2$ Dn PO$_5$ PVO$_1$ Op$_2$ VO$_1$ PVO$_2$	7	
	8.0	Br$_2$ Dn PO$_5$ PVO$_1$ Op$_2$ VO$_1$ PVO$_2$ PO$_1$ AOa$_1$	9	
B. suborbitale	4.1	Br$_2$	1	10.7
	8.3-9.2	Br$_2$ PO$_1$ PO$_2$	3	
	9.4	Br$_2$ PO$_1$ PO$_2$ Br$_1$ Br$_3$ Op$_2$	6	
	11.5	Br$_2$ PO$_1$ PO$_2$ Br$_1$ Br$_3$ Op$_2$ PO$_3$ PO$_4$ PO$_5$ AOa$_1$ AOa$_2$	11	

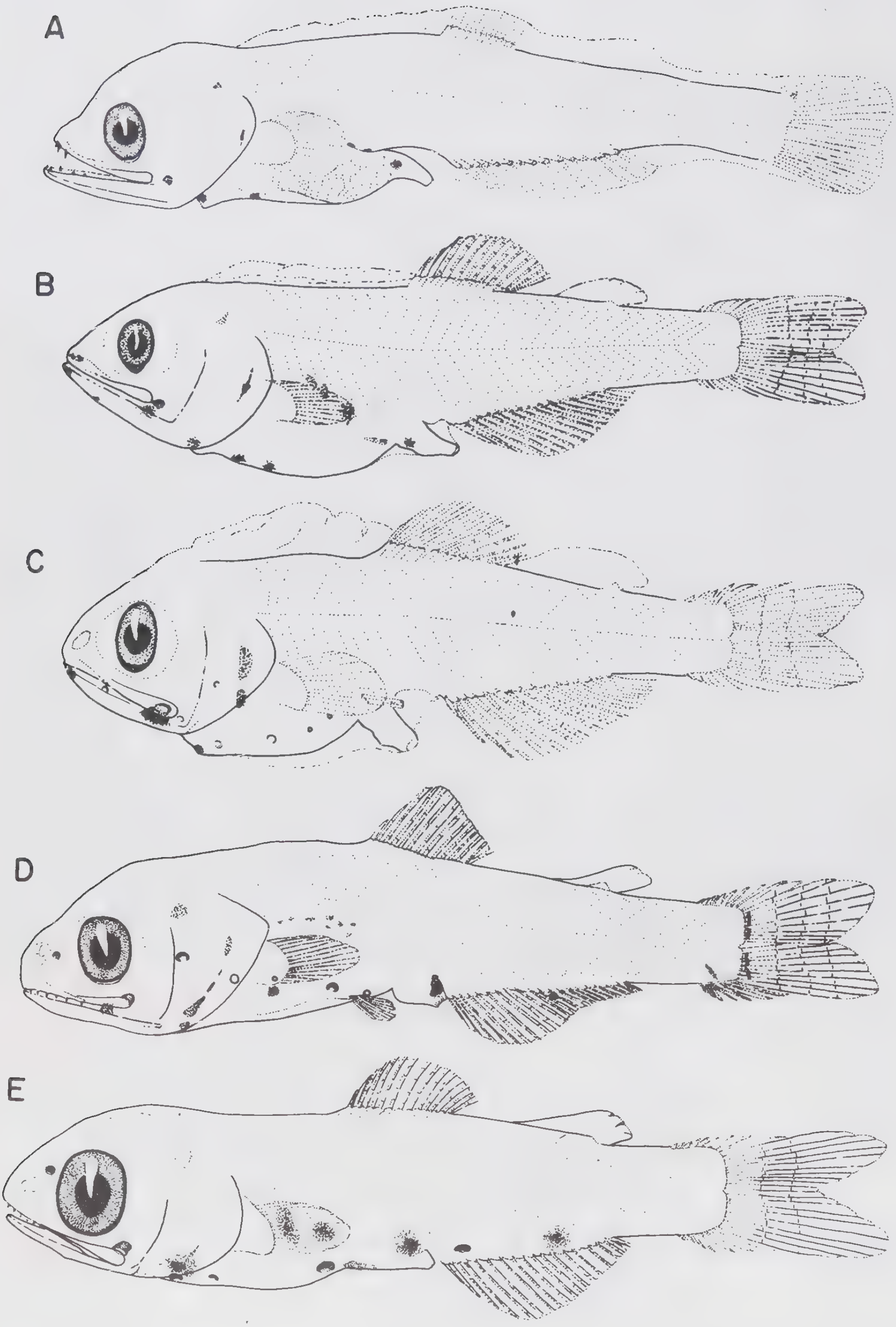

FIGURE 3.—Larvae of *Benthosema*. A. *B. glaciale,* 7.2 mm; B. *B. glaciale,* 10.5 mm; C. *B. suborbitale,* 9.2 mm; D. *B. pterota,* 8.5 mm; E. *B. fibulatum,* 8.7 mm.

larvae about 6.0 mm long. Thereafter the pattern diverges as shown in Table 1, but both species gradually add about a dozen pairs during the larval period. Specimens of *B. pterota* from the Persian Gulf off India, formed photophores at somewhat larger sizes than larvae of *B. panamense,* but in the same sequence. Transformation occurs at a small size, 10-12 mm in *B. panamense-pterota* and 11-13 mm in *B. fibulatum.*

Photophores appear relatively late in larvae of *B. suborbitale* and *B. glaciale,* however, the Br_1, Br_2, Op_2, and PO series appear in late larvae of both species (Table 1). Transformation occurs at about 9-11 mm in both species. The larvae of *B. panamense-pterota* and *B. fibulatum* are close to the larvae of *Diogenichthys* in several characters including body shape, gut shape, and early appearance of photophores.

As in *Benthosema,* the larval characters of *Hygophum* suggest some divergence within the genus, although all species have a highly characteristic series of isthmal melanophores, form the dorsal fin late in the larval period, and develop no photophores other than the Br_2, as larvae (Figure 4). The genus contains three divergent types of larvae. The most unusual of these are the extremely elongate larvae of *H. reinhardti* and *H. atratum,* which have very narrow eyes that are underlain by prominent choroid tissue and are borne on short stalks (Figure 4A). The amount of pigmentation along the gut and tail and on the myosepta and fin fold increases throughout the larval period.

A second larval type is represented by the largest number of species, *H. proximum, H. hygomi,* and *H. brunni,* all illustrated (Figure 4B-D), as well as *H. benoiti, H. hanseni,* and an undescribed form in our collection. These larvae are only moderately slender and have unstalked eyes of moderate width, subtended by prominent choroid tissue. Melanophores are located chiefly on the head and gut, however some species have pigment on the myosepta and fin fold. The trend in this group of species is for the early larval stages to have the heaviest pigment and for melanophores to be lost as development proceeds.

A third type of larva is exhibited by *H. macrochir, H. taaningi,* and an undescribed form in our collection (Figure 4E, F). These are relatively deep-bodied, have large, relatively wide eyes with little or no choroid tissue, and lack tail pigment. Also, the gut has a highly distinctive form; the anterior half has a very small diameter and opens dorsally into a prominent enlarged posterior section. In *H. macrochir* this enlarged section is covered with large melanophores. Larvae of this group occur only in the Atlantic.

The genus *Hygophum* affords an excellent example of the taxonomic utility of larval stages. The juveniles and adults of some species are notoriously difficult to identify. In contrast, the larvae of these species are highly distinct and can be readily identified. We have 11 such distinct larval types, whereas only 9 species are currently known for the adults. Search for adults of the two remaining larval types has led to the discovery of two undescribed species. In addition, characters of the adults of this genus reveal little about the relationships of the member species (Becker, 1965). A study of the larvae, however, shows that there are three highly distinct subgeneric groups, each containing from two to six closely related species. Such an independent view of the complete species complement of a genus is an invaluable tool in the formal revision of that genus.

Larvae of the species of *Symbolophorus* are perhaps the most cohesive of all myctophine genera (Figure 5A). In all species known to us the pectoral fin is large and is supported by an elongate aliform base. Also, the pelvic fins are large and develop earlier than in any other lanternfish genus. The narrow eyes have choroid tissue and are borne on short stalks. The amount of pigmentation decreases towards the end of the larval period. Most species attain a large size—up to 24 mm. The species differ principally in the size at which various larval structures appear.

The closely related genus, *Myctophum,* has a diversity of larval form unmatched in the family (Figures 5, 6, 7). Before taking up the bulk of the species in this genus we must first examine the most aberrant of all lanternfish larvae, that of *M. aurolaternatum* (Figure 5B). In this remarkable larva the eyes are borne on long stalks and the free trailing section of the gut is almost as long as the fish itself. The dorsal fin forms at the margin of the fin fold. These characters are so bizarre that it would seem preposterous to identify it as a lanternfish larva, much less that of *M. aurolaternatum.* Nonetheless, Å. Vedel Tåning first suggested the true identity of this larva (E. Bertelsen, pers. commun.) which we can now confirm since recently receiving the critical transforming specimens through the courtesy of Warren Freihofer (California Academy of Science). The uniqueness of this larva would certainly suggest

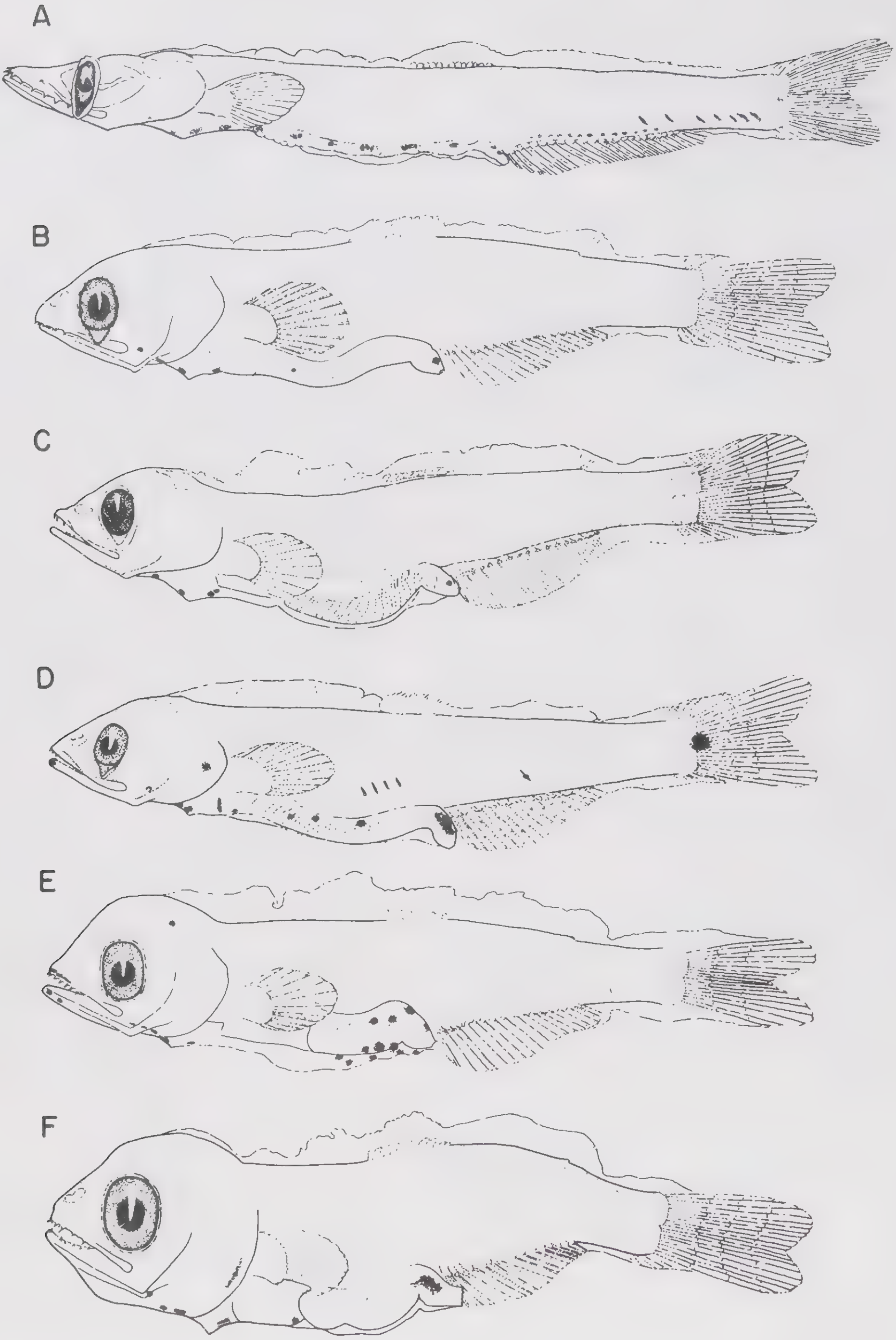

FIGURE 4.—Larvae of *Hygophum*. A. *H. reinhardti*, 12.8 mm; B. *H. proximum*, 8.9 mm; C. *H. hygomi*, 8.1 mm; D. *H. brunni*, 9.7 mm; E. *H. macrochir*, 7.3 mm; F. *H. taaningi*, 6.8 mm.

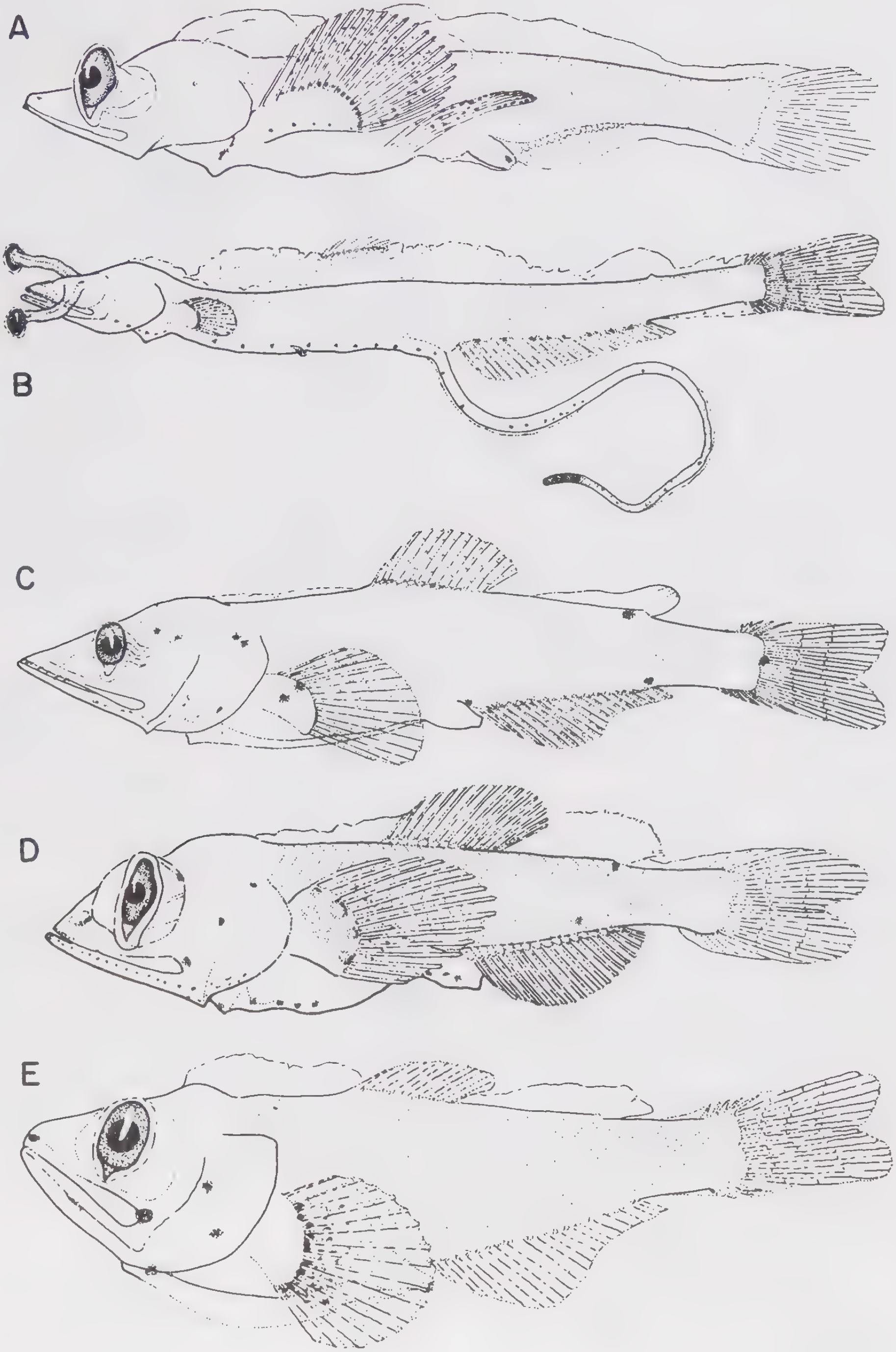

FIGURE 5.—Larvae of *Symbolophorus* and *Myctophum*. A. *S. californiense*, 9.6 mm; B. *M. aurolaternatum*, 26.0 mm; C. *M. punctatum*, 13.6 mm; D. *M. nitidulum*, 8.2 mm; E. *M. phengodes*, 9.8 mm.

the creation of a distinct genus for *M. aurolaternatum* and it is highly probable that corroborative characters will appear after careful reexamination of the adults.

With the removal of *M. aurolaternatum,* the remaining larvae of *Myctophum* form a diverse, yet recognizable, group. All have large broad pectoral fins supported on a highly characteristic fan-shaped base. The species may be divided into two groups, those which form only the Br_2 photophores and those which develop additional photophores during the larval period. In the first group the elongate larva of *M. punctatum* (Figure 5C) has stalked eyes and a slightly aliform pectoral fin base, reminiscent of *Symbolophorus* larvae, and may be the closest relative of that genus among the species of *Myctophum.* A closely related species, *M. nitidulum,* is also stalk-eyed, but is deeper-bodied, more heavily pigmented, and has a more fan-shaped pectoral fin base (Figure 5D). It is obvious from our studies that *M. nitidulum* is one member of a complex, that includes *M. affine* (not illustrated) and several other species. The lightly pigmented larva of *M. phengodes* has only a suggestion of stalked eyes but is similar in body shape to *M. nitidulum* (Figure 5E). The larval characters substantiate Paxton's (1972) decision to abolish the genus *Ctenoscopelus,* established for this species by Fraser-Brunner (1949).

The other major group of *Myctophum* is characterized by the appearance of the Dn photophore anterior to the eye, usually early in the larval period. These species fall into three rather distinct species groups on the basis of body and eye shape. The first is a group of four rotund broad-headed species, which have large unstalked eyes subtended by a short mass of choroid tissue. Of these, the larvae of *M. asperum* are the most heavily pigmented, particularly on the body (Figure 6A). Pigment is confined to the head in *M. obtusirostre,* is heavy under the posterior part of the gut in *Myctophum* sp. (possibly *brachygnathum*) and is developed on the jaws, branchistegal membrane and lower part of the pectoral fin base in *Myctophum* sp. (possibly *fissunovi*) as seen in Figure 6B-D. The latter three species form the PLO photophores on the pectoral fin base soon after the appearance of the Dn organs (Table 2).

Nafpaktitis (1973) has listed a number of characters for distinguishing adult *M. obtusirostre* from *M. brachygnathum.* He showed that *M. pristilepis* is a synonym of *M. brachygnathum.* The status of *M. imperceptum* Bekker and Borodulina has yet to be determined.

A second larval type is represented by *M. selenops* (Figure 7A) and a closely related species restricted to the Indian Ocean and Persian Gulf for which we can find no adult (Figure 7B). In these rotund species, the head is relatively longer and narrower than in the previous group and the slightly stalked eyes are narrower and bear more elongate choroid tissue. The two species differ in that the eyes of the unnamed larva are more definitely stalked than in *M. selenops.* Also the pigment pattern is markedly different, as is the size at which photophores appear. We have carefully examined larvae of *M. selenops* from the Atlantic, Indian, and Pacific Oceans, find them to be identical in all three oceans, and seriously question Wisner's (1971) allocation of the Hawaiian population as a distinct species, based on slight differences in relative eye size and SAO photophore orientation.

The third type of larvae that develop the Dn photophores is represented by *M. spinosum* (Figure 7C) and *M. lychnobium* (Figure 7D). These are elongate fusiform larvae with moderately narrow unstalked eyes, underlain by a pronounced choroid mass. *M. spinosum* is the more slender of the two and is extremely heavily pigmented, especially in older larvae. Pigmentation in *M. lychnobium* is confined to that in the illustrated

TABLE 2.—Sequence of photophore formation in species of *Myctophum* that form two or more pairs during the larval stage.

Species	Size range (mm)	Size at first formation (mm)				Size at transformation (mm)
		Br_2	Dn	PLO	PO_1	
M. asperum	ca. 3.0-9.8	4.2	4.6	9.8	—	Early transf. 11.4
M. obtusirostre	ca. 3.0-8.9	3.8	4.0	ca. 7.1	8.9	Late transf. 12.5
M. sp. (possibly *fissunovi*)	ca. 3.0-7.1	4.1	4.1	7.1	—	—
M. sp. (possibly *brachygnathum*)	6.0-11.4	6.0	6.0	ca. 9.0	ca. 9.0	Late transf. 13.8
M. lychnobium	3.5-12.1	ca. 6.0	6.3	12.1	—	Late transf. 14.2
M. spinosum	3.5-13.7	ca. 5.5	7.2	13.7	—	Late transf. 14.5
M. selenops	3.5-7.5	5.1	5.1	6.2	7.5	Late transf. 11.4
M. sp.	4.0-9.1	ca. 7.0	9.1	—	—	—

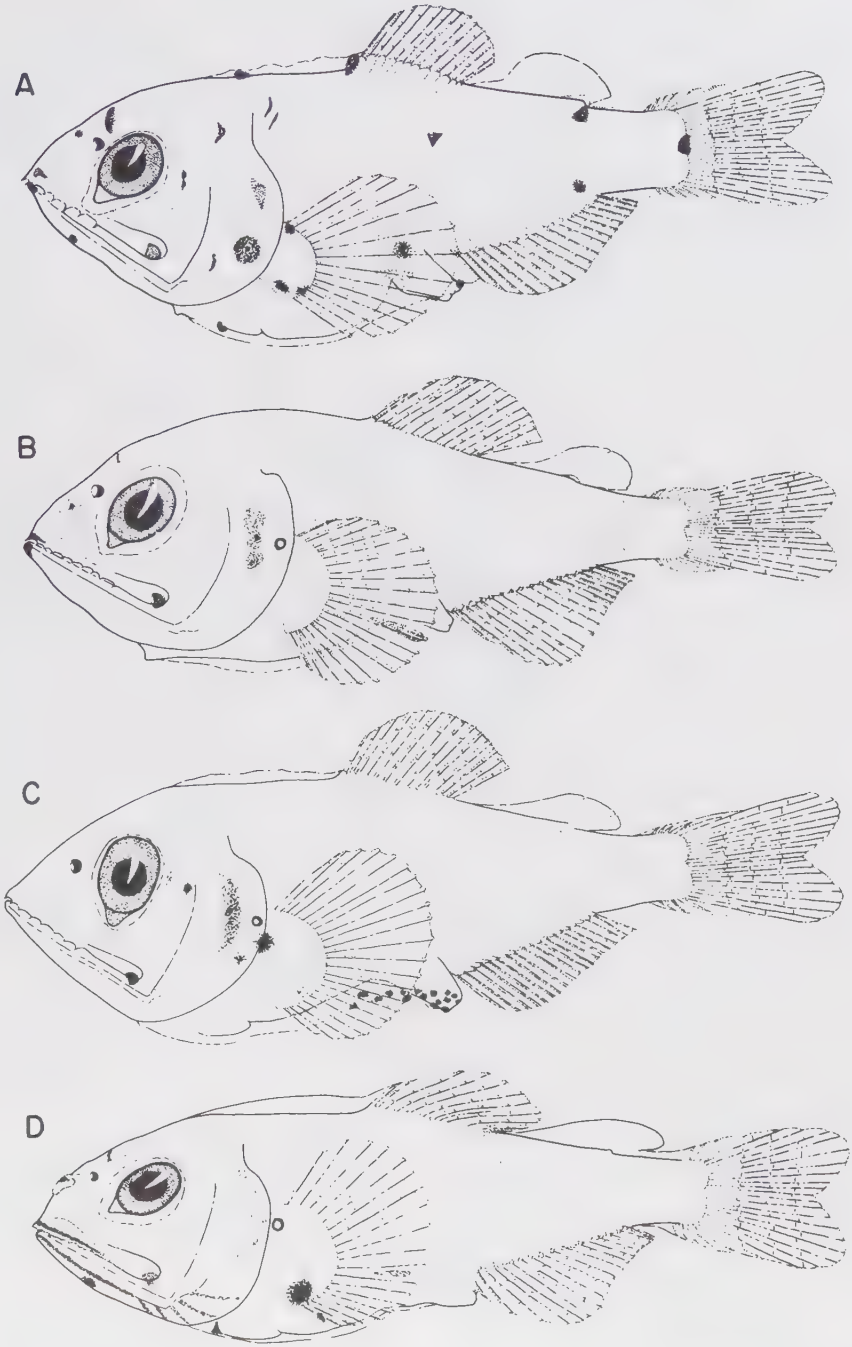

FIGURE 6.—Larvae of *Myctophum*. A. *M. asperum*, 6.8 mm; B. *M. obtusirostre*, 7.6 mm; C. *M.* sp. (possibly *brachygnathum*), 7.5 mm; D. *M.* sp. (possibly *fissunovi*), 7.4 mm.

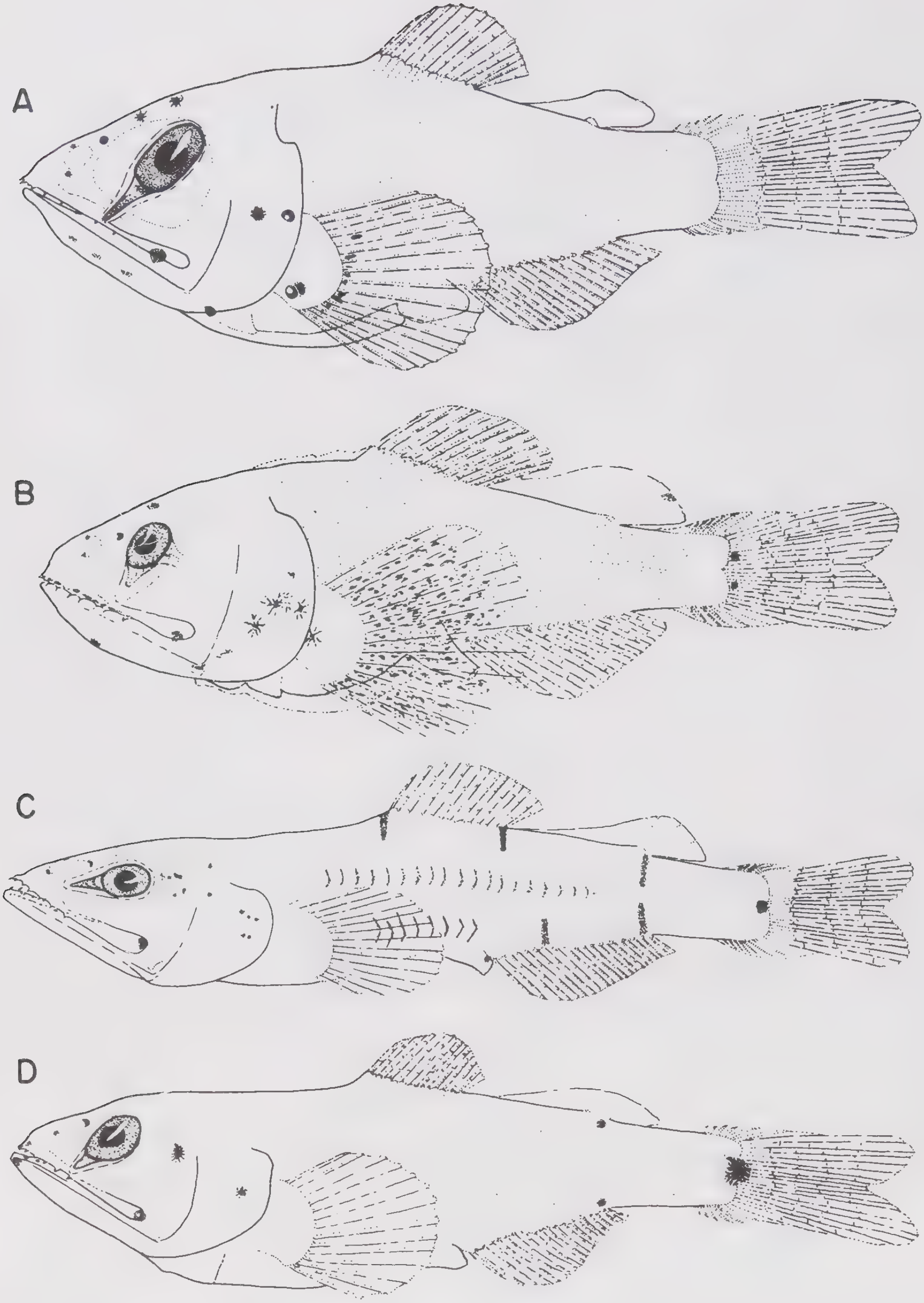

FIGURE 7.—Larvae of *Myctophum*. A. *M. selenops*, 7.8 mm; B. *M.* sp., 9.1 mm; C. *M. spinosum*, 9.0 mm; D. *M. lychnobium*, 9.5 mm.

specimen. Only larvae of *M. lychnobium* have been taken in the eastern Pacific, whereas both species have been taken in the central and western Pacific and in the Indian Ocean. Taxonomists dealing with adult characters only, have placed *M. lychnobium* in synonymy with *M. spinosum* but the distinctiveness of the larvae suggests that the adult characters should be reexamined.

The larvae of *M. spinosum* and *M. lychnobium,* although clearly developing the Dn pair of photophores, resemble the larvae of *M. punctatum* in body shape and pigmentation, a species which does not develop the Dn as larvae. Actually, there are some common characters of pigmentation and eye structure which appear in all of the groups of *Myctophum* species described above. What we appear to be dealing with is a mosaic of larval characters in a highly complex genus. The taxonomy of *Myctophum* presently is confused; our work on the larvae should help define the number of species in the genus and, perhaps, adult characters will emerge that can be combined with larval characters to define the phyletic lines within the genus.

Larvae of the four genera known collectively as the slendertailed myctophids are shown in Figure 8. Quite obviously there are two highly divergent generic pairs. *Loweina* and *Tarletonbeania* are characterized by large oval eyes, posterior placement of median fins to accommodate the immense fin fold, and elongated lower pectoral rays bearing spatulate processes. *Gonichthys* and *Centrobranchus* are characterized by a deep but markedly compressed head and body and small narrow eyes with extremely elongate choroid tissue. As stated earlier, the larval characters suggest strongly that the two generic pairs are not closely related and should not be grouped into a tribe. The *Gonichthys-Centrobranchus* pair is similar in eye shape and gut shape to some species of *Myctophum,* however no species of *Myctophum* even approaches this pair in body shape. The characters of the other pair are so divergent as to give no clue of their affinities within the subfamily Myctophinae.

THE SUBFAMILY LAMPANYCTINAE

The subfamily Lampanyctinae is considerably larger than the Myctophinae; it contains about 19 genera and 200-250 species compared with 12 genera and about 75 species in the Myctophinae. Paxton (1972) divided the genera into four tribes on the basis of a combination of osteological features and characters of the photophores. In a previous paper (Moser and Ahlstrom, 1972) we discussed Paxton's placement of genera in these tribes and indicated that the larval characters suggested a somewhat different distribution of genera among the four tribes. For the purposes of this discussion the tribes referred to here are those suggested by the larval characters.

In general, the larvae of the Lampanyctinae are much less diverse in larval characters and specializations than are the larvae of the Myctophinae, although exceptions to this may be found in two of the lampanyctine tribes, the Diaphini and the Lampanyctini.

The tribe Diaphini is made up of two genera —*Diaphus* contains about 50 species and *Lobianchia* has 3 species. Both genera develop photophores, in addition to the Br_2, during the larval period; in fact more are developed in *Diaphus* than in any other lanternfish genus.

There are two basic larval types in *Diaphus* (Figure 9A, B). One has a slender body, small head, and a series of persistent melanophores on the ventral midline of the tail. The other type has a deeper body, bulbous head, and a single persistent ventral tail melanophore, or none. It is exceptional for larvae of either type to develop pigment on the head and it never occurs between the eyes, as is common in *Lampanyctus*. Both types do form embedded melanophores at the base of the caudal fin rays.

The slender type is restricted to the species that develop a suborbital photophore as adults (*Diaphus* sensu stricto of Fraser-Brunner, 1949) and is represented in Figure 9A by *D. theta*. The stubby type is represented by *D. pacificus* (Figure 9B). The specimens illustrated for the two species are rather early larval stages which have not yet formed their larval photophores, other than the Br_2. The first additional pair to form in both types is the PO_5 and then the PO_1 (Table 3). The large genus *Diaphus,* except for the Atlantic species ably reviewed by Nafpaktitis (1968), is in a state of taxonomic confusion. Various workers (Fraser-Brunner, 1949; Bolin, 1959) have attempted to split the genus into smaller, more cohesive groups; the larval evidence would suggest that at least two divergent groups are present.

The larvae of the three species of *Lobianchia* are

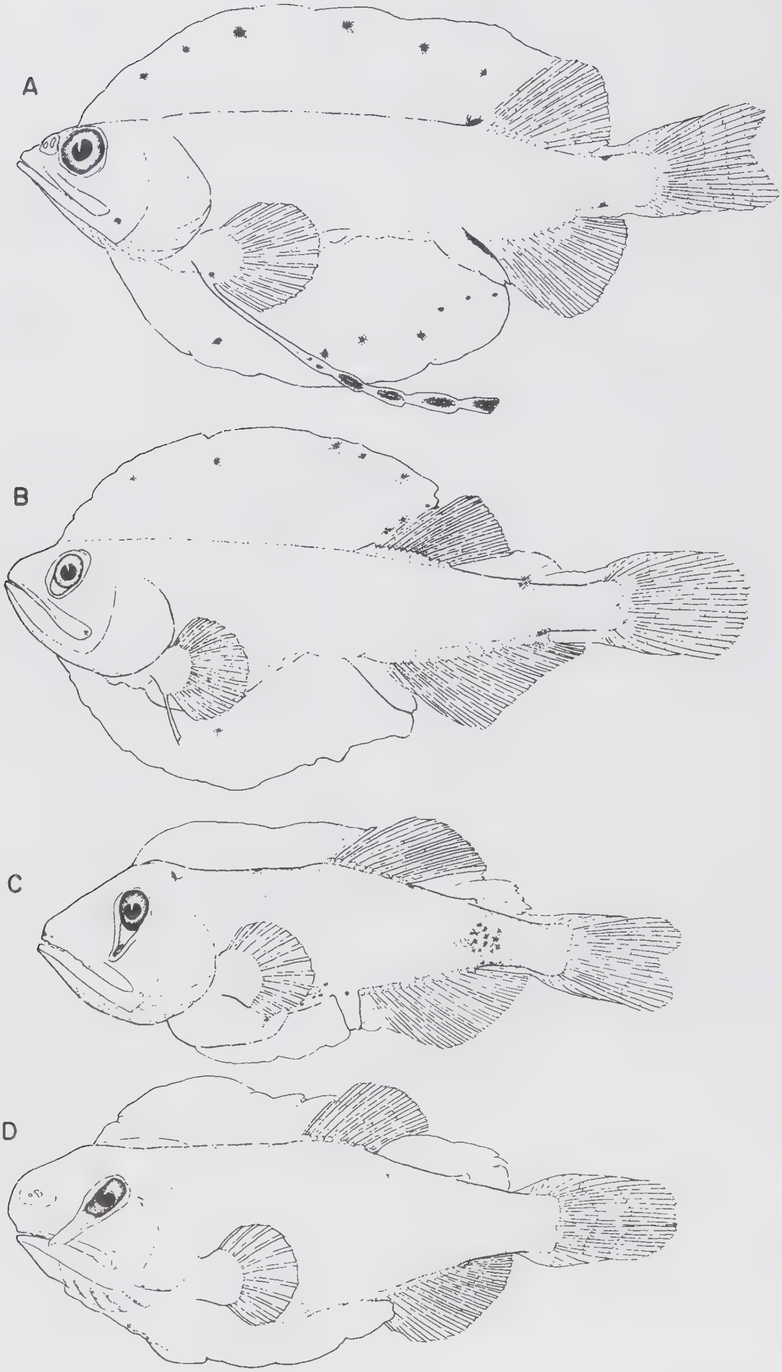

FIGURE 8.—Larvae of Gonichthyini. A. *Loweina rara*, 17.6 mm; B. *Tarletonbeania crenularis*, 18.9 mm; C. *Gonichthys tenuiculus*, 7.7 mm; D. *Centrobranchus choerocephalus*, 7.3 mm.

larvae about 6.0 mm long. Thereafter the pattern diverges as shown in Table 1, but both species gradually add about a dozen pairs during the larval period. Specimens of *B. pterota* from the Persian Gulf off India, formed photophores at somewhat larger sizes than larvae of *B. panamense*, but in the same sequence. Transformation occurs at a small size, 10-12 mm in *B. panamense-pterota* and 11-13 mm in *B. fibulatum*.

Photophores appear relatively late in larvae of *B. suborbitale* and *B. glaciale*, however, the Br_1, Br_2, Op_2, and PO series appear in late larvae of both species (Table 1). Transformation occurs at about 9-11 mm in both species. The larvae of *B. panamense-pterota* and *B. fibulatum* are close to the larvae of *Diogenichthys* in several characters including body shape, gut shape, and early appearance of photophores.

As in *Benthosema*, the larval characters of *Hygophum* suggest some divergence within the genus, although all species have a highly characteristic series of isthmal melanophores, form the dorsal fin late in the larval period, and develop no photophores other than the Br_2, as larvae (Figure 4). The genus contains three divergent types of larvae. The most unusual of these are the extremely elongate larvae of *H. reinhardti* and *H. atratum*, which have very narrow eyes that are underlain by prominent choroid tissue and are borne on short stalks (Figure 4A). The amount of pigmentation along the gut and tail and on the myosepta and fin fold increases throughout the larval period.

A second larval type is represented by the largest number of species, *H. proximum*, *H. hygomi*, and *H. brunni*, all illustrated (Figure 4B-D), as well as *H. benoiti*, *H. hanseni*, and an undescribed form in our collection. These larvae are only moderately slender and have unstalked eyes of moderate width, subtended by prominent choroid tissue. Melanophores are located chiefly on the head and gut, however some species have pigment on the myosepta and fin fold. The trend in this group of species is for the early larval stages to have the heaviest pigment and for melanophores to be lost as development proceeds.

A third type of larva is exhibited by *H. macrochir*, *H. taaningi*, and an undescribed form in our collection (Figure 4E, F). These are relatively deep-bodied, have large, relatively wide eyes with little or no choroid tissue, and lack tail pigment. Also, the gut has a highly distinctive form; the anterior half has a very small diameter and opens dorsally into a prominent enlarged posterior section. In *H. macrochir* this enlarged section is covered with large melanophores. Larvae of this group occur only in the Atlantic.

The genus *Hygophum* affords an excellent example of the taxonomic utility of larval stages. The juveniles and adults of some species are notoriously difficult to identify. In contrast, the larvae of these species are highly distinct and can be readily identified. We have 11 such distinct larval types, whereas only 9 species are currently known for the adults. Search for adults of the two remaining larval types has led to the discovery of two undescribed species. In addition, characters of the adults of this genus reveal little about the relationships of the member species (Becker, 1965). A study of the larvae, however, shows that there are three highly distinct subgeneric groups, each containing from two to six closely related species. Such an independent view of the complete species complement of a genus is an invaluable tool in the formal revision of that genus.

Larvae of the species of *Symbolophorus* are perhaps the most cohesive of all myctophine genera (Figure 5A). In all species known to us the pectoral fin is large and is supported by an elongate aliform base. Also, the pelvic fins are large and develop earlier than in any other lanternfish genus. The narrow eyes have choroid tissue and are borne on short stalks. The amount of pigmentation decreases towards the end of the larval period. Most species attain a large size—up to 24 mm. The species differ principally in the size at which various larval structures appear.

The closely related genus, *Myctophum*, has a diversity of larval form unmatched in the family (Figures 5, 6, 7). Before taking up the bulk of the species in this genus we must first examine the most aberrant of all lanternfish larvae, that of *M. aurolaternatum* (Figure 5B). In this remarkable larva the eyes are borne on long stalks and the free trailing section of the gut is almost as long as the fish itself. The dorsal fin forms at the margin of the fin fold. These characters are so bizarre that it would seem preposterous to identify it as a lanternfish larva, much less that of *M. aurolaternatum*. Nonetheless, Å. Vedel Tåning first suggested the true identity of this larva (E. Bertelsen, pers. commun.) which we can now confirm since recently receiving the critical transforming specimens through the courtesy of Warren Freihofer (California Academy of Science). The uniqueness of this larva would certainly suggest

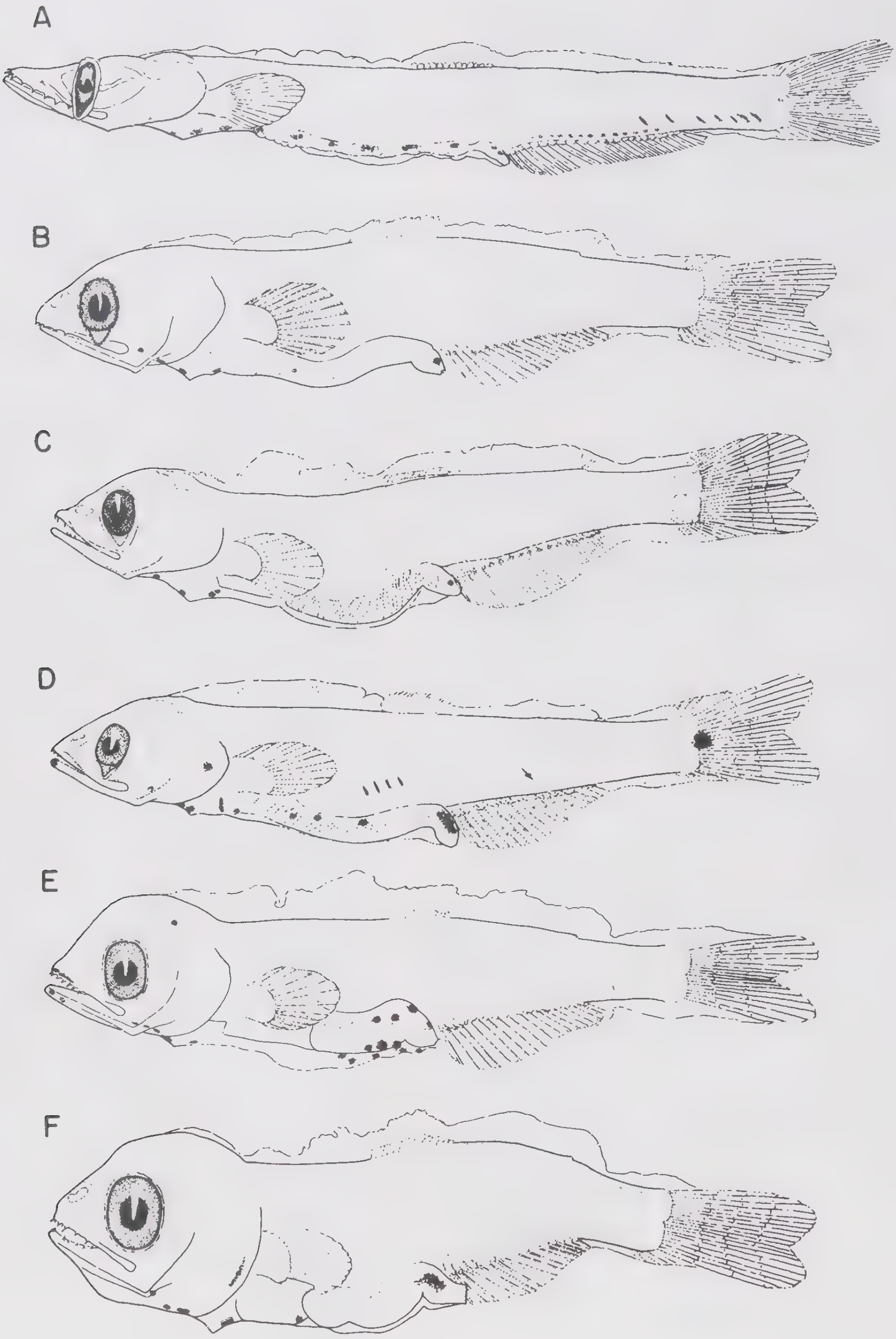

FIGURE 4.—Larvae of *Hygophum*. A. *H. reinhardti*, 12.8 mm; B. *H. proximum*, 8.9 mm; C. *H. hygomi*, 8.1 mm; D. *H. brunni*, 9.7 mm; E. *H. macrochir*, 7.3 mm; F. *H. taaningi*, 6.8 mm.

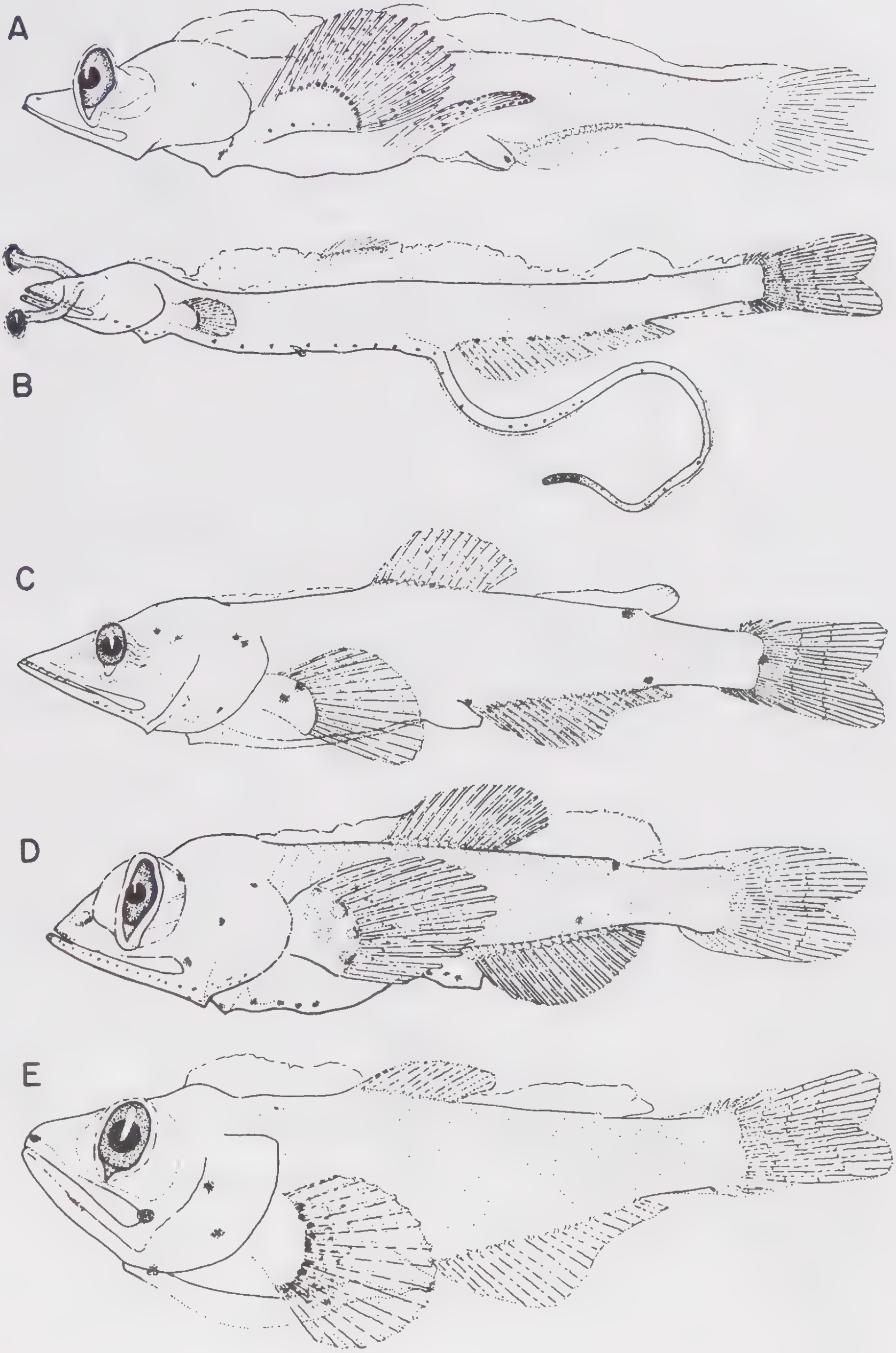

FIGURE 5.—Larvae of *Symbolophorus* and *Myctophum*. A. *S. californiense*, 9.6 mm; B. *M. aurolaternatum*, 26.0 mm; C. *M. punctatum*, 13.6 mm; D. *M. nitidulum*, 8.2 mm; E. *M. phengodes*, 9.8 mm.

the creation of a distinct genus for *M. aurolaternatum* and it is highly probable that corroborative characters will appear after careful reexamination of the adults.

With the removal of *M. aurolaternatum,* the remaining larvae of *Myctophum* form a diverse, yet recognizable, group. All have large broad pectoral fins supported on a highly characteristic fan-shaped base. The species may be divided into two groups, those which form only the Br_2 photophores and those which develop additional photophores during the larval period. In the first group the elongate larva of *M. punctatum* (Figure 5C) has stalked eyes and a slightly aliform pectoral fin base, reminiscent of *Symbolophorus* larvae, and may be the closest relative of that genus among the species of *Myctophum.* A closely related species, *M. nitidulum,* is also stalk-eyed, but is deeper-bodied, more heavily pigmented, and has a more fan-shaped pectoral fin base (Figure 5D). It is obvious from our studies that *M. nitidulum* is one member of a complex, that includes *M. affine* (not illustrated) and several other species. The lightly pigmented larva of *M. phengodes* has only a suggestion of stalked eyes but is similar in body shape to *M. nitidulum* (Figure 5E). The larval characters substantiate Paxton's (1972) decision to abolish the genus *Ctenoscopelus,* established for this species by Fraser-Brunner (1949).

The other major group of *Myctophum* is characterized by the appearance of the Dn photophore anterior to the eye, usually early in the larval period. These species fall into three rather distinct species groups on the basis of body and eye shape. The first is a group of four rotund broad-headed species, which have large unstalked eyes subtended by a short mass of choroid tissue. Of these, the larvae of *M. asperum* are the most heavily pigmented, particularly on the body (Figure 6A). Pigment is confined to the head in *M. obtusirostre,* is heavy under the posterior part of the gut in *Myctophum* sp. (possibly *brachygnathum*) and is developed on the jaws, branchistegal membrane and lower part of the pectoral fin base in *Myctophum* sp. (possibly *fissunovi*) as seen in Figure 6B-D. The latter three species form the PLO photophores on the pectoral fin base soon after the appearance of the Dn organs (Table 2).

Nafpaktitis (1973) has listed a number of characters for distinguishing adult *M. obtusirostre* from *M. brachygnathum.* He showed that *M. pristilepis* is a synonym of *M. brachygnathum.* The status of *M. imperceptum* Bekker and Borodulina has yet to be determined.

A second larval type is represented by *M. selenops* (Figure 7A) and a closely related species restricted to the Indian Ocean and Persian Gulf for which we can find no adult (Figure 7B). In these rotund species, the head is relatively longer and narrower than in the previous group and the slightly stalked eyes are narrower and bear more elongate choroid tissue. The two species differ in that the eyes of the unnamed larva are more definitely stalked than in *M. selenops.* Also the pigment pattern is markedly different, as is the size at which photophores appear. We have carefully examined larvae of *M. selenops* from the Atlantic, Indian, and Pacific Oceans, find them to be identical in all three oceans, and seriously question Wisner's (1971) allocation of the Hawaiian population as a distinct species, based on slight differences in relative eye size and SAO photophore orientation.

The third type of larvae that develop the Dn photophores is represented by *M. spinosum* (Figure 7C) and *M. lychnobium* (Figure 7D). These are elongate fusiform larvae with moderately narrow unstalked eyes, underlain by a pronounced choroid mass. *M. spinosum* is the more slender of the two and is extremely heavily pigmented, especially in older larvae. Pigmentation in *M. lychnobium* is confined to that in the illustrated

TABLE 2.—Sequence of photophore formation in species of *Myctophum* that form two or more pairs during the larval stage.

Species	Size range (mm)	Size at first formation (mm)				Size at transformation (mm)
		Br_2	Dn	PLO	PO_1	
M. asperum	ca. 3.0-9.8	4.2	4.6	9.8	—	Early transf. 11.4
M. obtusirostre	ca. 3.0-8.9	3.8	4.0	ca. 7.1	8.9	Late transf. 12.5
M. sp. (possibly *fissunovi*)	ca. 3.0-7.1	4.1	4.1	7.1	—	—
M. sp. (possibly *brachygnathum*)	6.0-11.4	6.0	6.0	ca. 9.0	ca. 9.0	Late transf. 13.8
M. lychnobium	3.5-12.1	ca. 6.0	6.3	12.1	—	Late transf. 14.2
M. spinosum	3.5-13.7	ca. 5.5	7.2	13.7	—	Late transf. 14.5
M. selenops	3.5-7.5	5.1	5.1	6.2	7.5	Late transf. 11.4
M. sp.	4.0-9.1	ca. 7.0	9.1	—	—	—

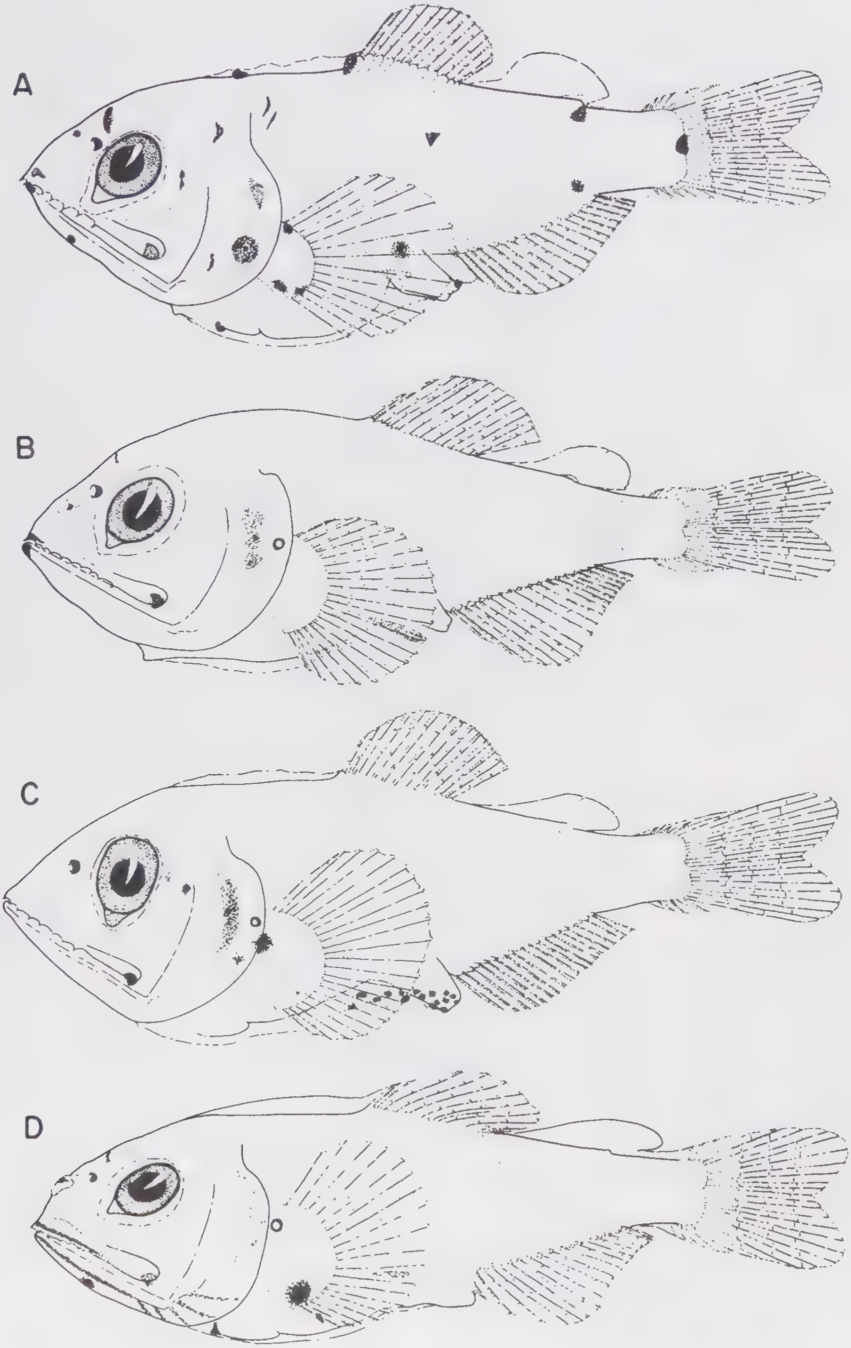

FIGURE 6.—Larvae of *Myctophum*. A. *M. asperum*, 6.8 mm; B. *M. obtusirostre*, 7.6 mm; C. *M.* sp. (possibly *brachygnathum*), 7.5 mm; D. *M.* sp. (possibly *fissunovi*), 7.4 mm.

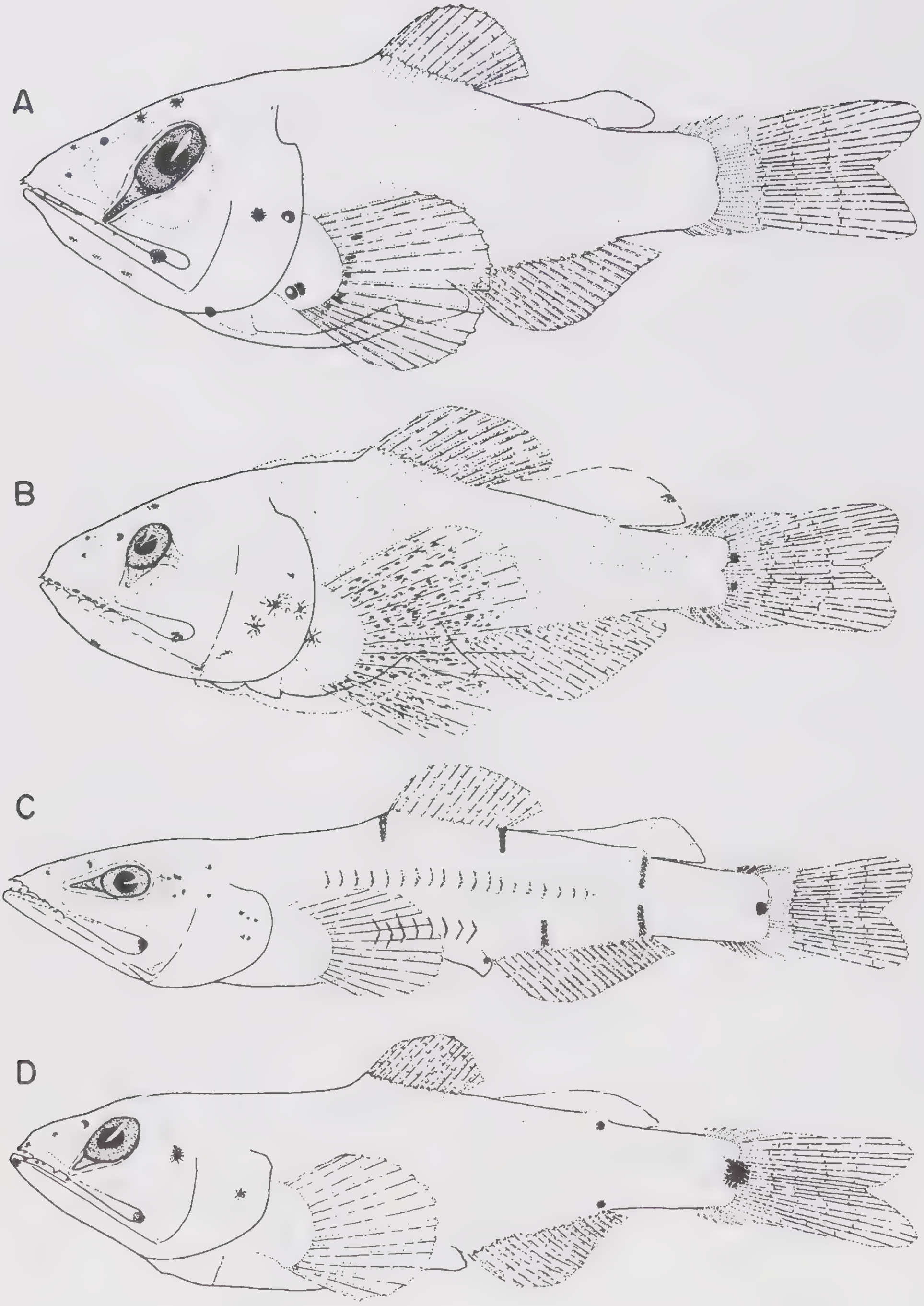

FIGURE 7.—Larvae of *Myctophum*. A. *M. selenops*, 7.8 mm; B. *M.* sp., 9.1 mm; C. *M. spinosum*, 9.0 mm; D. *M. lychnobium*, 9.5 mm.

specimen. Only larvae of *M. lychnobium* have been taken in the eastern Pacific, whereas both species have been taken in the central and western Pacific and in the Indian Ocean. Taxonomists dealing with adult characters only, have placed *M. lychnobium* in synonymy with *M. spinosum* but the distinctiveness of the larvae suggests that the adult characters should be reexamined.

The larvae of *M. spinosum* and *M. lychnobium*, although clearly developing the Dn pair of photophores, resemble the larvae of *M. punctatum* in body shape and pigmentation, a species which does not develop the Dn as larvae. Actually, there are some common characters of pigmentation and eye structure which appear in all of the groups of *Myctophum* species described above. What we appear to be dealing with is a mosaic of larval characters in a highly complex genus. The taxonomy of *Myctophum* presently is confused; our work on the larvae should help define the number of species in the genus and, perhaps, adult characters will emerge that can be combined with larval characters to define the phyletic lines within the genus.

Larvae of the four genera known collectively as the slendertailed myctophids are shown in Figure 8. Quite obviously there are two highly divergent generic pairs. *Loweina* and *Tarletonbeania* are characterized by large oval eyes, posterior placement of median fins to accommodate the immense fin fold, and elongated lower pectoral rays bearing spatulate processes. *Gonichthys* and *Centrobranchus* are characterized by a deep but markedly compressed head and body and small narrow eyes with extremely elongate choroid tissue. As stated earlier, the larval characters suggest strongly that the two generic pairs are not closely related and should not be grouped into a tribe. The *Gonichthys-Centrobranchus* pair is similar in eye shape and gut shape to some species of *Myctophum,* however no species of *Myctophum* even approaches this pair in body shape. The characters of the other pair are so divergent as to give no clue of their affinities within the subfamily Myctophinae.

THE SUBFAMILY LAMPANYCTINAE

The subfamily Lampanyctinae is considerably larger than the Myctophinae; it contains about 19 genera and 200-250 species compared with 12 genera and about 75 species in the Myctophinae. Paxton (1972) divided the genera into four tribes on the basis of a combination of osteological features and characters of the photophores. In a previous paper (Moser and Ahlstrom, 1972) we discussed Paxton's placement of genera in these tribes and indicated that the larval characters suggested a somewhat different distribution of genera among the four tribes. For the purposes of this discussion the tribes referred to here are those suggested by the larval characters.

In general, the larvae of the Lampanyctinae are much less diverse in larval characters and specializations than are the larvae of the Myctophinae, although exceptions to this may be found in two of the lampanyctine tribes, the Diaphini and the Lampanyctini.

The tribe Diaphini is made up of two genera —*Diaphus* contains about 50 species and *Lobianchia* has 3 species. Both genera develop photophores, in addition to the Br_2, during the larval period; in fact more are developed in *Diaphus* than in any other lanternfish genus.

There are two basic larval types in *Diaphus* (Figure 9A, B). One has a slender body, small head, and a series of persistent melanophores on the ventral midline of the tail. The other type has a deeper body, bulbous head, and a single persistent ventral tail melanophore, or none. It is exceptional for larvae of either type to develop pigment on the head and it never occurs between the eyes, as is common in *Lampanyctus*. Both types do form embedded melanophores at the base of the caudal fin rays.

The slender type is restricted to the species that develop a suborbital photophore as adults (*Diaphus* sensu stricto of Fraser-Brunner, 1949) and is represented in Figure 9A by *D. theta*. The stubby type is represented by *D. pacificus* (Figure 9B). The specimens illustrated for the two species are rather early larval stages which have not yet formed their larval photophores, other than the Br_2. The first additional pair to form in both types is the PO_5 and then the PO_1 (Table 3). The large genus *Diaphus,* except for the Atlantic species ably reviewed by Nafpaktitis (1968), is in a state of taxonomic confusion. Various workers (Fraser-Brunner, 1949; Bolin, 1959) have attempted to split the genus into smaller, more cohesive groups; the larval evidence would suggest that at least two divergent groups are present.

The larvae of the three species of *Lobianchia* are

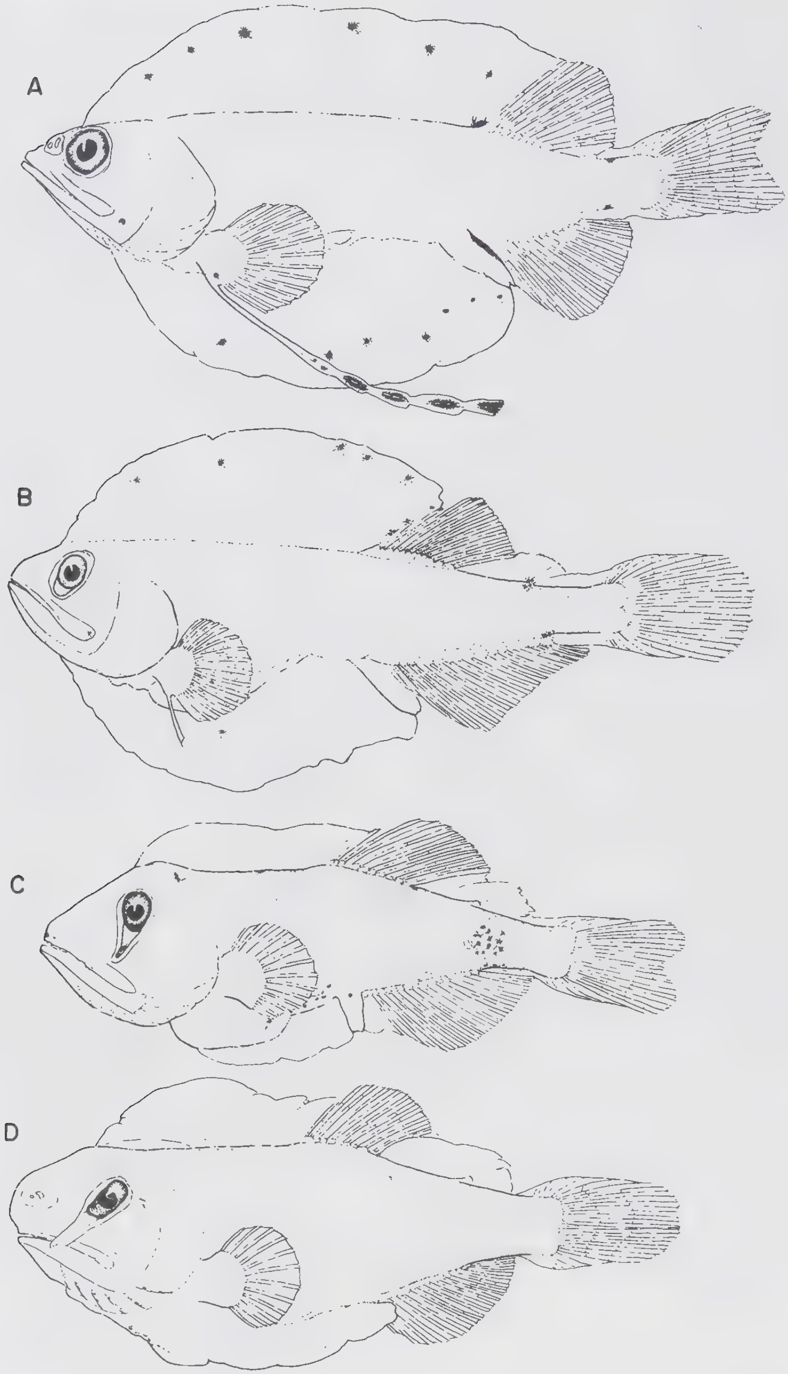

FIGURE 8.—Larvae of Gonichthyini. A. *Loweina rara*, 17.6 mm; B. *Tarletonbeania crenularis*, 18.9 mm; C. *Gonichthys tenuiculus*, 7.7 mm; D. *Centrobranchus choerocephalus*, 7.3 mm.

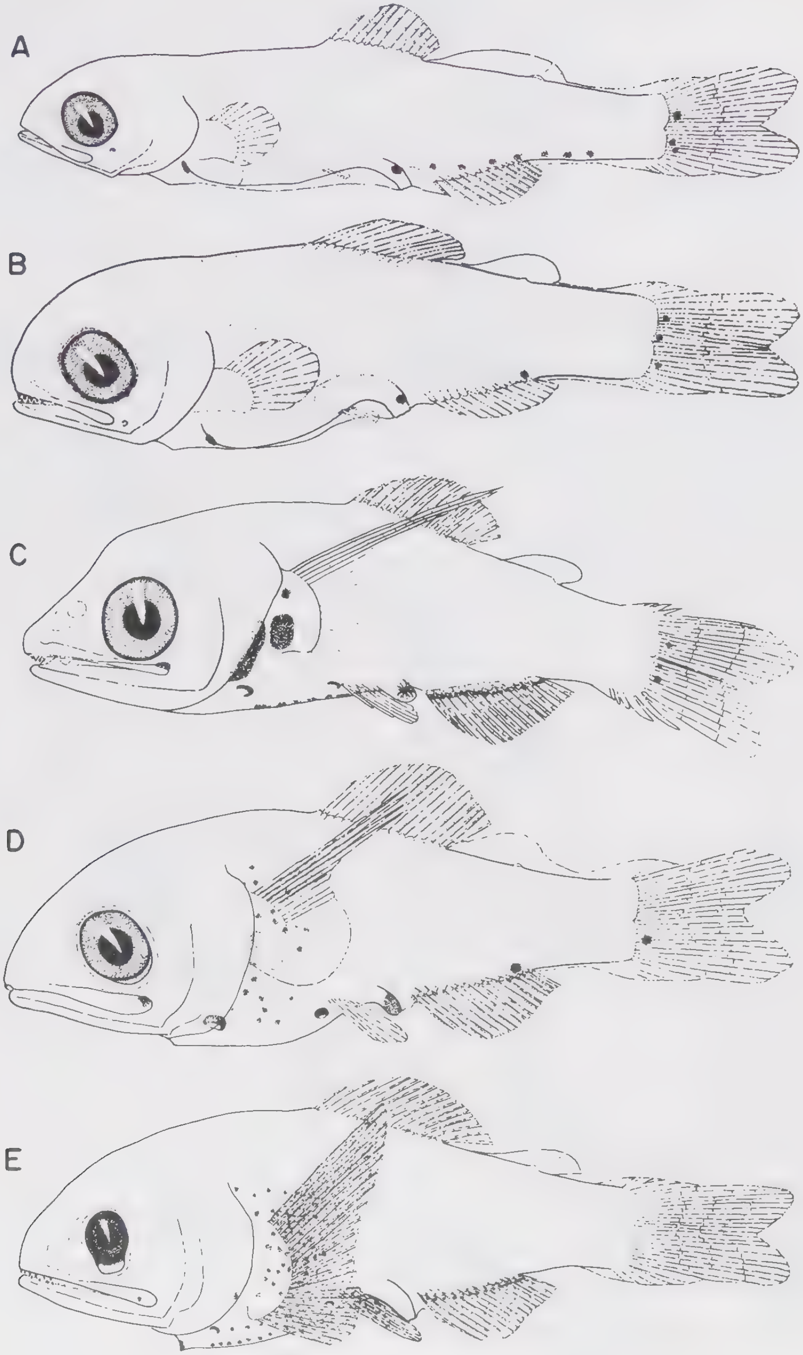

FIGURE 9.—Larvae of *Diaphus* and *Lobianchia*. A. *D. theta*, 6.9 mm; B. *D. pacificus*, 5.2 mm; C. *L. urolampus*, 7.2 mm; D. *L. gemellari*, 6.7 mm; E. *L. dofleini*, 8.2 mm.

TABLE 3.—Sequence of photophore formation in larvae of two species of *Diaphus*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
D. theta	6.2	Br_2 PO_5	2	ca. 12.0
	7.6	Br_2 PO_5 PO_1	3	
	8.2	Br_2 PO_5 PO_1 VO_1	4	
	8.6	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2	6	
	9.0	Br_2 PO_5 PO_1 VO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5	9	
	9.2	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5 VLO	10	
D. pacificus	5.7	Br_2 PO_5 PO_1	3	9.8
	6.2	Br_2 PO_5 PO_1 PO_2 PVO_1	5	
	6.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3	6	
	7.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3 VO_1	7	

deep-bodied, have large broad heads, and are easily identified by their unique wing-shaped pectoral fins (Figure 9C-E). The larvae of all three species are heavily pigmented and develop the Br_2, PO_1, and PO_5 photophores sequentially. In *L. urolampus* (Figure 9C) and *L. gemellari* (Figure 9D) the eyes are large and nearly round and the lower pectoral rays are delayed in developing. In *L. dofleini* the lower pectoral rays develop along with the produced upper rays and the eye is completely different (Figure 9E). With its narrow elliptical shape and unique squarish mass of choroid tissue, it is the single obvious exception to the rule of narrow eyes in the subfamily Myctophinae and rounded eyes in the Lampanyctinae. All other larval characters identify this species as a *Lobianchia,* and we conclude that the narrowing of the eye in this species occurred independently as a secondary adaptation.

In our view the tribe Lampanyctini contains the genera *Lampanyctus, Triphoturus, Stenobrachius,* and *Parvilux.* As recently as Fraser-Brunner's (1949) review of the family Myctophidae, *Lampanyctus* was still a catchall genus with a number of disparate subgenera. Since then the subgenera *Stenobrachius, Triphoturus,* and *Lepidophanes* have been removed from *Lampanyctus* and afforded generic status. *Lepidophanes* has been further split into the genera *Lepidophanes* and *Bolinichthys.* All of the separated genera have distinctive larval morphs. With their removal, the species of *Lampanyctus* form a more coherent assemblage of 40-50 species, and despite the diversity of larval specializations encountered in the genus, there is a central morph and pattern of larval development.

Lampanyctus larvae are deep-bodied and bigheaded. In older larvae characteristic pigment can develop at a variety of locations such as the tip of the lower jaw, between the eyes, the back of the head, the side of the head, the adipose fin, the pectoral fin, internally in the region of the cleithra, and along the myosepta. The pigment patterns are of prime importance in identifying the larvae to species.

There are several rather distinct larval types in *Lampanyctus.* One of these consists of a group of species whose adults are characterized by having the pectoral fins much reduced or even absent, and has been separated recently as a distinct genus *Paralampanyctus* by Kotthaus (1972) with *P. niger* as type. Previously, Günther (1887) had proposed the generic name *Nannobrachium* for this species and this has priority over *Paralampanyctus* (John Paxton, pers. commun.). There is a remarkable trend of jaw specialization in the larvae of this group (Figure 10). The larva of *L. ritteri* has jaws of moderate length and the other species shown have progressively longer jaws with more prominent teeth, particularly anteriorly. This trend culminates in the larva of *Lampanyctus* sp. (possibly *achirus*) which somewhat resembles a larval billfish. This species will lack the pectoral fin in juveniles and adults, even though it is well developed in the larvae. The pectoral fins are also large in *L. regalis* and *L. niger* larvae, but will be small and weakly developed in adults. This disparity is even more apparent in another eastern Pacific species, which lacks pectoral fins as an adult, but whose larvae have the largest pectoral fins with the highest number of rays that we have encountered among *Lampanyctus* larvae. Other less spectacular specializations appear in the other subgroups of *Lampanyctus,* but it appears that the larval characters will be helpful in defining the species composition of the several subgenera.

Representatives of other genera of Lampanyctini, *Triphoturus, Stenobrachius,* and *Parvilux* are illustrated in Figure 11A-C. Small larvae of *Triphoturus* and *Stenobrachius* have a row of melanophores along the ventral margin of the tail

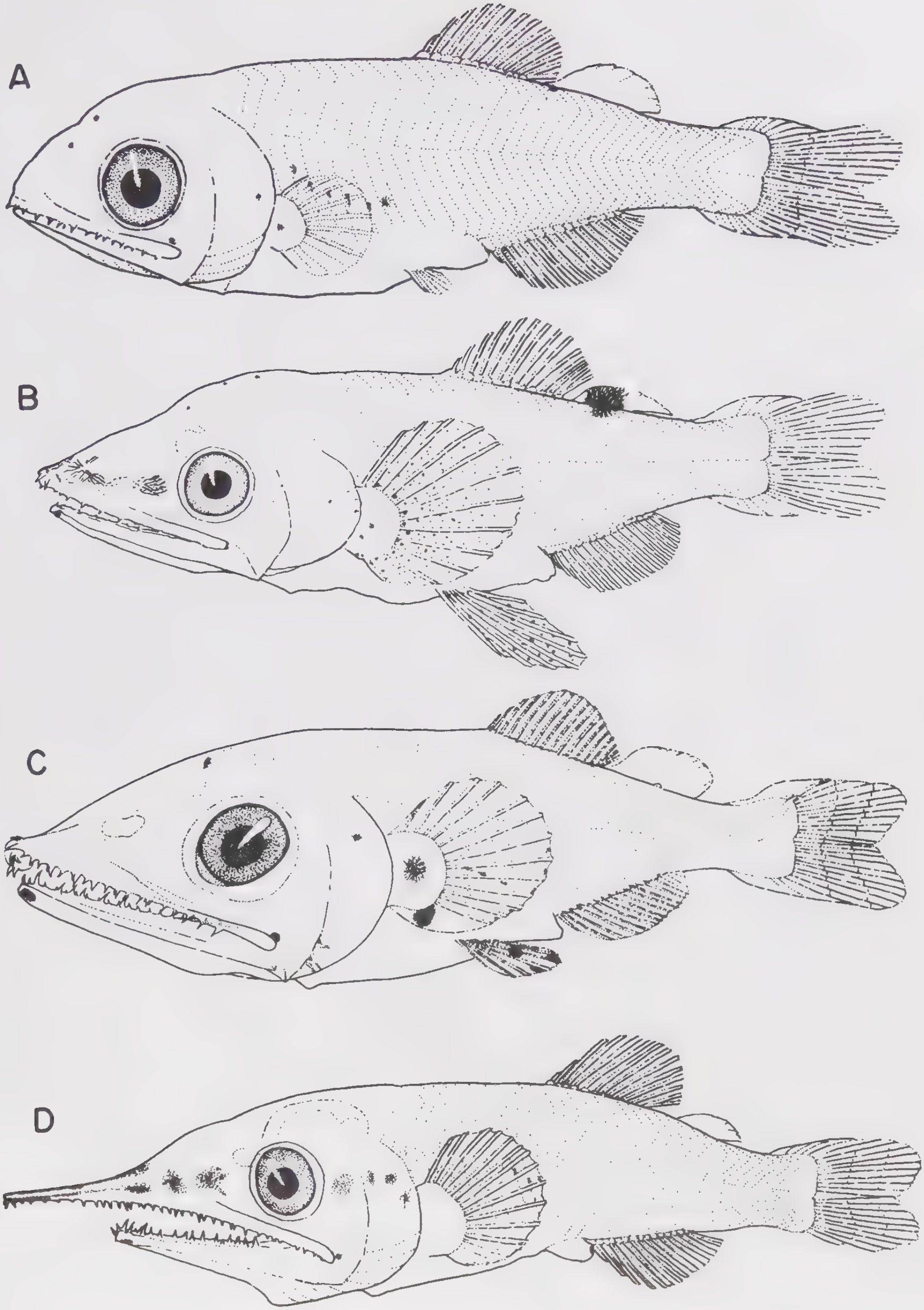

FIGURE 10.—Larvae of *Lampanyctus*. A. *L. ritteri*, 10.1 mm; B. *L. regalis*, 9.1 mm; C. *L. niger*, 8.7 mm; D. *L.* sp. (possibly *achirus*), 13.4 mm.

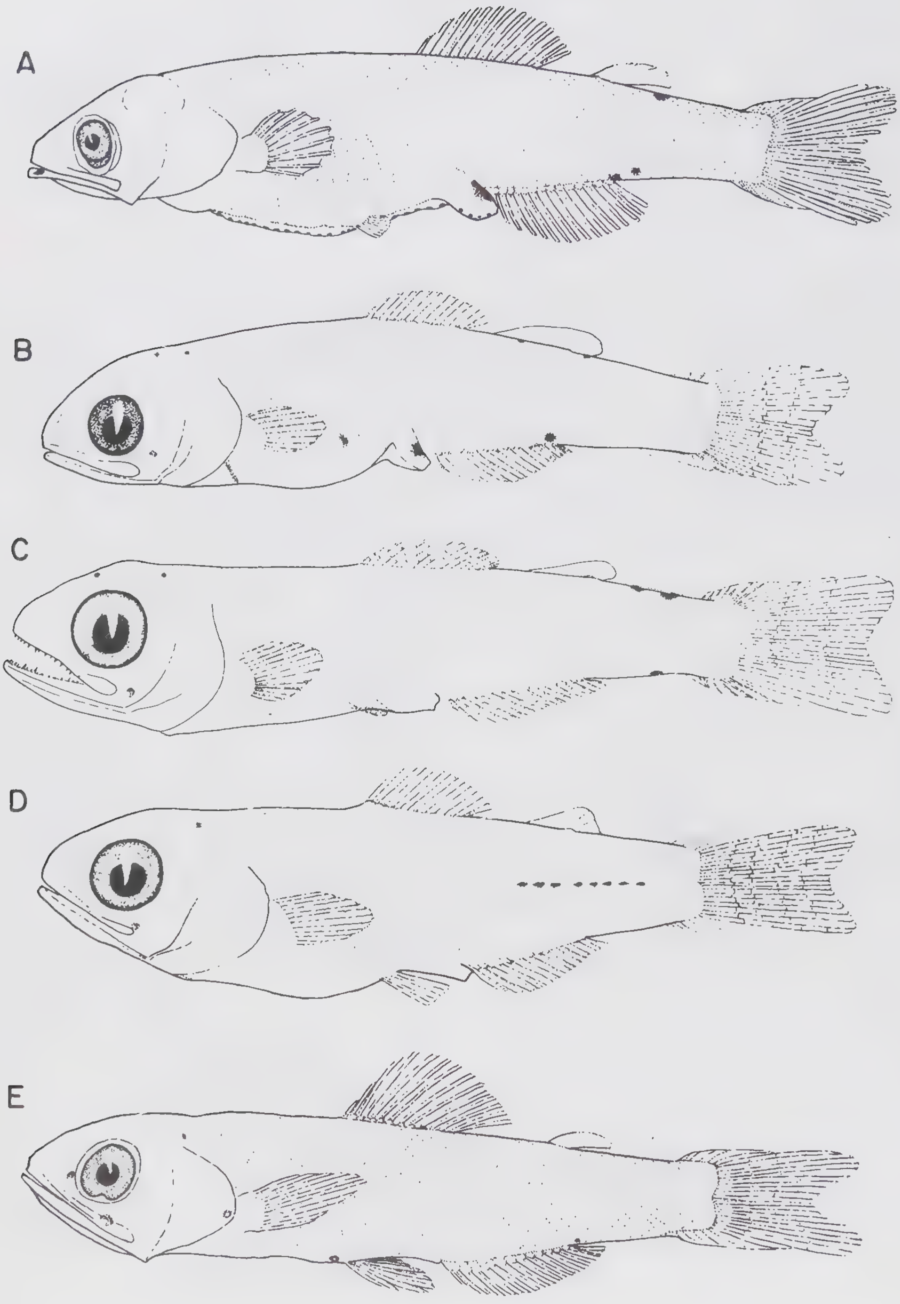

FIGURE 11.—Larvae of Lampanyctini and Gymnoscopelini. A. *Triphoturus mexicanus*, 10.5 mm; B. *Stenobrachius leucopsarus*, 10.4 mm; C. *Parvilux ingens*, 14.4 mm; D. *Bolinichthys supralateralis*, 9.4 mm; E. *Ceratoscopelus townsendi*, 16.6 mm.

but these coalesce into one or two spots in midstage larvae. *Triphoturus* larvae are characterized further by their distinctive head shape and by the series of melanophores along the ventral midline below the gut. *Stenobrachius* larvae add considerable pigment late in the larval period, particularly along the dorsum and on the myosepta of the trunk. The larvae of *Parvilux* are distinct in shape and pigmentation. Paxton (1972) placed this genus in *Lampanyctus* based on osteological characters. In certain photophore arrangements, however, particularly in the posterior placement of the VLO and the nonangulate arrangement of the SAO, the genus appears to us to be more closely related to *Stenobrachius* than to *Lampanyctus*. These characters in addition to the distinctness of the larvae would suggest that the validity of *Parvilux* should be reconsidered.

The tribe Gymnoscopelini judged from larval and/or adult characters contains a dozen genera (*Notoscopelus, Lampichthys, Scopelopsis, Ceratoscopelus, Lepidophanes, Bolinichthys, Lampadena, Taaningichthys, Dorsadena, Lampanyctodes, Gymnoscopelus,* and *Hintonia*). The larvae of these genera are united by a group of common characters, including a distinctive, usually slender, body outline, a series of melanophores on the dorsal and ventral midlines of the tail (in most genera), and the development of a group of photophores during the larval period, most notably the PO_5, PLO, and Vn. The larvae of this tribe were treated extensively in a previous paper with representative larvae illustrated for 10 of the 12 genera (Moser and Ahlstrom, 1972). Additional species of *Bolinichthys (B. supralateralis,* Figure 11D), *Ceratoscopelus (C. townsendi,* Figure 11E), *Lampadena (L. luminosa,* Figure 12B), *Lepidophanes (L. gaussi,* Figure 12C) are illustrated herein. Illustrations of *Notoscopelus resplendens* (Figure 12A) and *Scopelopsis multipunctatus* (Figure 12D) are included for comparative purposes. It need only be mentioned here that the clusters of closely related genera within this tribe are readily apparent from examining the larval characters, especially the sequence of photophore development, and these groupings agree closely with those established on the basis of adult characters.

The species *Notolychnus valdiviae* has so many unique adult characters that Paxton (1972) assigned it to the monotypic tribe *Notolychnini*. Likewise the larva has a number of unusual characters (Figure 12E). The shape of the eye is variable from specimen to specimen; it can be narrow and elliptical or nearly round, but most typically would be classified as irregular in shape. The shape of the head, body, and gut is unusual and distinctive. The larval characters are of little help in elucidating the affinities of this species within the Myctophidae and, when added to the list of unique adult characters, only magnify the problem. It would seem to make just as much sense to establish a separate subfamily for *Notolychnus* as to place it in a monotypic tribe in the subfamily Lampanyctinae.

The larvae illustrated in this paper comprise 55 species representing 24 genera. Illustrations are included for larvae of 11 of the 12 genera in the subfamily Myctophinae; not included are illustrations of *Diogenichthys* (see Moser and Ahlstrom, 1970 for *D. laternatus* and *D. atlanticus*). In the subfamily Lampanyctinae larvae are illustrated for 13 of the 19 genera. The omitted genera (*Lampichthys, Lampanyctodes, Gymnoscopelus,* and *Tanningichthys*), all from the tribe Gymnoscopelini, are illustrated in Moser and Ahlstrom (1972). Larvae of *Hintonia* and *Dorsadena* have not yet been identified.

SOME EVOLUTIONARY CONSIDERATIONS

With this brief review of lanternfish larvae completed, let us now turn to an interesting problem of myctophid evolution to which study of the larvae may contribute importantly—the evolution of photophore pattern. With a single exception, all adult myctophids have two conspicuous rows of photophores that extend the length of the body on each side of the ventral midline. The photophores are grouped and positioned in a definite and often diagnostic pattern. Also, lanternfishes have a specific pattern of photophores on the sides of the body, below the lateral line, and on the ventral aspect of the head. The exception is *Taaningichthys paurolychnus,* which appears to lack body photophores entirely. In addition to these photophores, some lanternfish genera have photophores positioned in a pattern above the lateral line and some have small "secondary" photophores distributed more generally over regions of the body and head. Another type of luminous structure present on most myctophids are discrete glands located at the caudal peduncle. Typically, these are sexually dimorphic in character and, doubtless, play some part in courtship

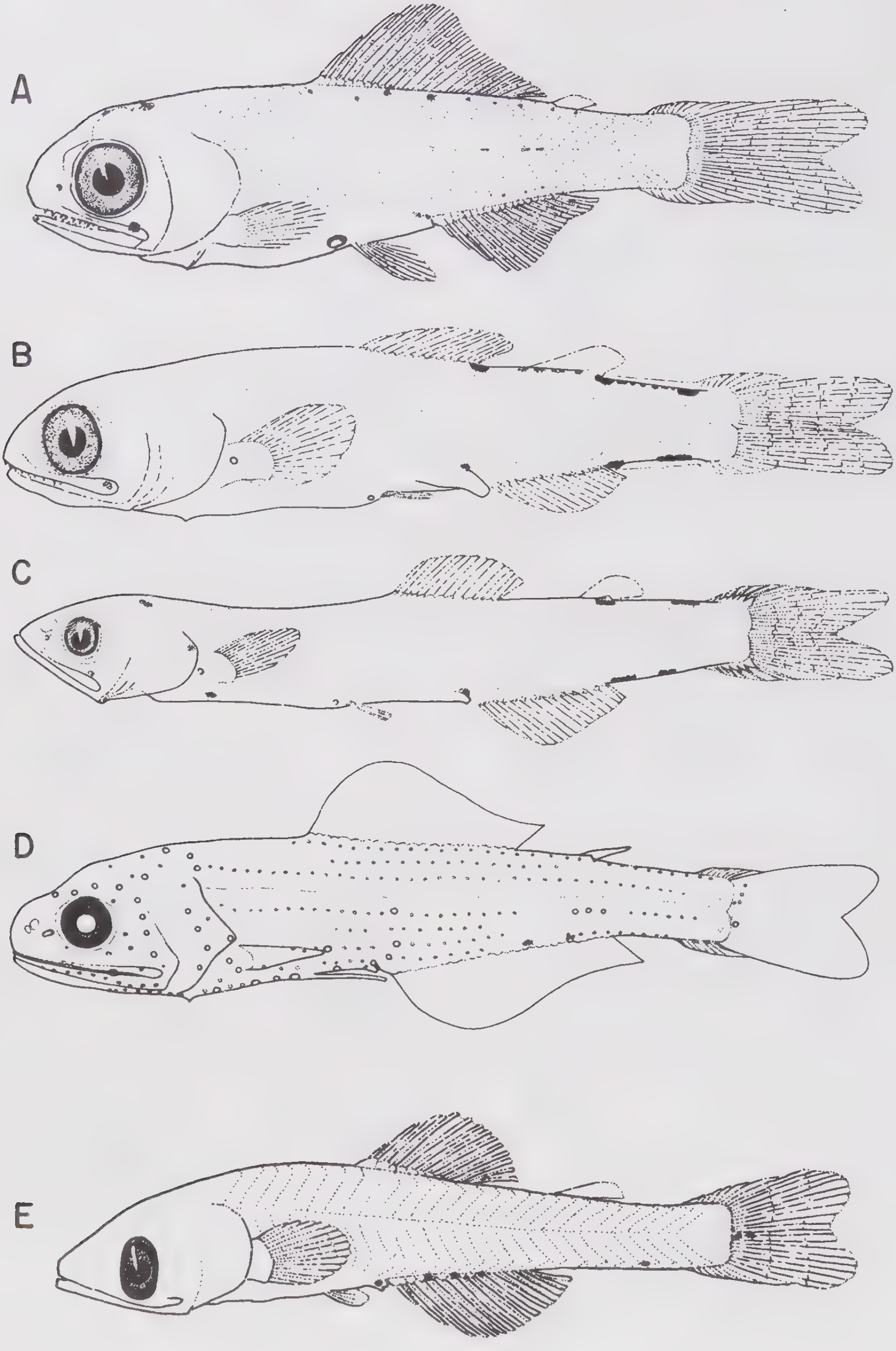

FIGURE 12.—Larvae of Gymnoscopelini and Notolychnini. A. *Notoscopelus resplendens*, 11.2 mm; B. *Lampadena luminosa*, 12.8 mm; C. *Lepidophanes gaussi*, 13.5 mm; D. *Scopelopsis multipunctatus*, 17.5 mm; E. *Notolychnus valdiviae*, 9.2 mm.

behavior. Finally, some myctophids have small patches of soft whitish, apparently luminous, tissue located at various regions of the body.

The most popular speculation as to the possible function of the patterns of photophores and luminous scales is that they function in species recognition (see McAllister, 1967). An explanation for the universality of the two ventral rows was postulated by Clarke (1963). His suggestion that these downward directed rows emit a continuous light of ambient wavelength, which conceals the fish from deeper-living predators by countershading, has much appeal.

We have long been interested in the mechanism by which such patterns of photophores could have evolved and believe we have gained some insight into this mechanism through our studies of the larval stages. Our proposal, as expressed in an earlier paper (Moser and Ahlstrom, 1972), is that ancestral myctophids had a generalized arrangement of unspecialized photophores, one at the posterior margin of each scale pocket, and a group of similar photophores on the head. We further proposed that the specific photophore patterns of contemporary myctophids evolved through progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the unspecialized photophores. This idea came to us upon discovering the remarkable transforming specimens of *Scopelopsis multipunctatus,* the adults of which have a small photophore at each scale pocket and a group of photophores on the head. In the adults, the "primary" organs can be distinguished only by their modified lens-bearing scales, but in the transforming specimens (Figure 11D) the primary photophores stand out clearly as enlarged members of the meristic series of light organs. It struck us that a similar arrangement of photophores might have existed in the adults of an ancestral species, and led to the development of our ideas on the evolution of photophore pattern. Our theory was further strengthened by neurological findings and by what we feel are inherent weaknesses in Bolin's (1939) and Fraser-Brunner's (1949) theory that photophore patterns evolved by the upward migration of organs from ventral rows of photophores.

Viewed from the standpoint of our theory the subfamily Myctophinae would be considered highly specialized, since it is here that diminution of secondary photophores has reached its highest degree; they are totally lacking in the subfamily. The individual "primary" photophores are typically highly developed and concentrated ventrally on the body. The ventral location of photophores in Myctophinae is probably related to their habitat. That is, they are generally shallow-living active fishes that have well–developed gas bladders and it is plausible that concentration of photophores ventrally on the body evolved as an adaptation for countershading and protection from deeper-living predators. This view of the Myctophinae is completely contrary to those previously held for this subfamily. On the basis of the "upward migration" theory of photophore evolution, myctophines were thought to be primitive unspecialized forms. Formerly, we too subscribed to this view, and contrasting the then supposed primitive features such as low photophore position and short jaws of the adults with the highly specialized and diverse features of the larvae, we proposed that the evolutionary pace had differed in the larval and adult stages of the subfamily. Our altered opinion would view both larvae and adults of the Myctophinae as highly advanced and would interpret the low photophores, prominent gas bladders, short jaws, and often narrow caudal peduncles as specialized adaptations of active surface-dwelling fishes.

Our view of the Lampanyctinae must also be revamped. Formerly we considered the diverse and often dorsally oriented pattern of photophores and accessary luminous tissue to be highly specialized features. Possibly, the luminous scalelike patches and luminous glands are specialized adaptations, but we feel that the presence of small secondary photophores and the dorsal positioning of primary photophores in many of the genera, indicate a retention of the ancestral condition. The Lampanyctinae are generally deeper-living than the Myctophinae and many genera are lethargic fishes that rest vertically in the water column (Barham, 1970). In deeper-living fishes with such a behavior pattern there would be little evolutionary advantage in having ventrally concentrated photophores, and the fat-invested swim bladders and long jaws typical of many genera could have evolved in relation to habitat and activity pattern. It is interesting that the most obvious exception in the subfamily, the Diaphini, are active, often surface-dwelling fishes with relatively short jaws and ventrally concentrated photophores. It is obvious from the present paper that the larvae of Lampanyctinae exhibit much less diversity than the Myctophinae, but we no longer view the adult myctophines as being more "primitive" than the adult lampanyctines. We feel that the adults of both subfamilies are equally specialized and that these specializations are basically related to their particular habitat.

In summary, thorough study of the larvae of a teleost family such as the Myctophidae can be most helpful in species validation, in analyzing affinities at all taxon levels, and in assessing phylogenetic lineages. Also, the above discussion would indicate that larval studies can provide interesting insights into the major directions of evolution within a family of fish.

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DISTRIBUTION AND ABUNDANCE OF FISH EGGS AND LARVAE IN THE GULF OF CALIFORNIA

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INTRODUCTION

From time to time during its 24 year history the oceanographic cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) have extended beyond the California Current system. One example is the multivessel NORPAC Expedition which encompassed much of the northeast Pacific in 1955. Another such example is the series of seven oceanographic cruises made into the Gulf of California during 1956 and 1957.

Ships and personnel from the National Marine Fisheries Service (NMFS) and Scripps Institution of Oceanography (SIO) took part in the seven cruises, employing methods described by Kramer et al. (1972). On the first of these cruises (5602) the NMFS vessel BLACK DOUGLAS occupied 93 stations from the mouth of the Gulf northward as far as Tiburón Island from February 6 to 18, 1956 (Figure 1). On the second cruise (5604) the BLACK DOUGLAS occupied 129 stations throughout the full length of the Gulf from 8 to 24 April, 1956. On the third cruise (5612) the SIO vessel HORIZON occupied an abbreviated set of 79 stations, primarily on the western side of the Gulf and as far north as Tiburón Island from December 3 to 17, 1956. On cruise 5702 the SIO vessel SPENCER F. BAIRD occupied 70 stations as far northward as Tiburón Island February 9–20, 1957 (Figure 3). The remaining cruises in 1957 (Figure 3) each occupied a pattern of stations throughout the entire Gulf. On cruise 5704 the BLACK DOUGLAS occupied 125 stations from 7 to 22 April. The SIO vessel STRANGER occupied 132 stations on cruise 5706 from June 9 to 23.

The oceanographic observations from these cruises have been published by Scripps Institution of Oceanography (1963, 1965). Except for Ahlstrom's illustration of the distribution of Pacific mackerel on cruise 5602 (Ahlstrom, 1956, Figure 21), the data on the fish eggs and larvae have never been reported, largely because their identification has been accomplished over a long period, when time has permitted diversion from the task of identifying eggs and larvae from regular CalCOFI cruises. It is the purpose of this paper to give an overview of the seasonal abundance of the fish larvae collected on six of these cruises (5602–5706) and to give the patterns of geographic distribution for the abundant species which are important as commercial or forage fishes. Eggs of the Pacific mackerel and sardine were identified for three cruises (5602, 5604, 5702) and are used to estimate the spawning biomass of these species for those years. Finally the distribution and abundance of fish larvae is discussed in relation to the special oceanographic conditions in the Gulf and in relation to zoogeographic patterns of the subtropical and tropical northeast Pacific. Before embarking on this, however, it would be useful to review briefly the environmental characteristics of the Gulf of California and to give some general background information on its ichthyofauna.

This unique body of water is bounded by arid Baja California on the west and the Mexican states of Sonora and Sinaloa on the east. It extends about 1400 km between latitudes 23 and 32 north and has an average width of about 150 km. Wegener (1922) proposed that the Gulf was formed by the separation of Baja California from the Mexican mainland, a supposition which has been strengthened by recent investigations into sea floor spreading in that region (Elders et al., 1972). The northern ⅓ of the Gulf is separated

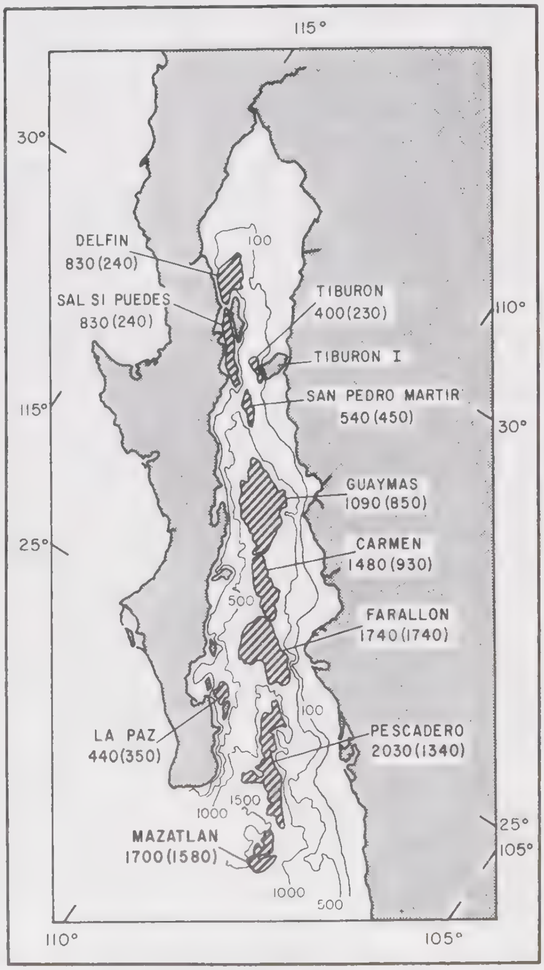

FIGURE 1. Basins of the Gulf of California with their maximum depths and sill depths (fathoms). Redrawn from van Andel (1964) and depth data from same publication.

from the lower part by two large islands, Ángel de la Guarda and Tiburón. Except for two basins, Delfín and Sal si Puedes shown in Figure 1, the head of the Gulf is shallow, with an average depth of about 200 m. Alluvial deposits, largely from the Colorado River, have filled the trough in this region to produce a smooth concave sea floor. This contrasts sharply with the bathymetry south of Tiburón and Ángel de la Guarda, which is characterized by a series of deep basins (down to 3000 m) running along the axis of the trough. These basins are separated by transverse sills of about 1500 m depth and the entire series is separated from the shallow Delfín and Sal si Puedes basins by a shallow sill of 200–250 m. The coastal features of the eastern and western sides of the Gulf are in sharp contrast. The Baja California coast south of Ángel de la Guarda is characterized by steep rocky escarpments broken occasionally by sandy beaches and by two major bays, Bahía La Paz and Bahía Concepción. Bordering the coastline is a linear series of small rocky islands. The sandy beaches become more extensive north of Bahía Concepción and are almost unbroken in the north. The eastern shoreline of the Gulf, except for a region of rocky headlands between Bahía Kino and Guaymas, is characterized by a wider shelf than is found on the western shore and by extensive beaches of sand or mud.

What is known about the oceanography of the Gulf has been reviewed in a series of papers by Roden (1958), Roden and Groves (1959), and Roden (1964). Situated between arid and mountainous Baja California on the west and the arid mainland to the east, it is an evaporation basin with highly saline and generally warm surface waters. Surface salinities show a general increase from south to north with a range of 34.8‰ to 36‰ but there is little seasonal variation for any given latitude. Surface temperatures, however, show a very large seasonal range that increases from about 9°C at the Gulf entrance to about 16°C at the head of the Gulf. Composite tidal range also increases markedly from south to north in the Gulf. From the Gulf entrance to Tiburón the increase is only slight with a spring range of about 1½ m. North of Tiburón the range increases rapidly to a maximum spring range of 10 m at the mouth of the Colorado River. This strong tidal mixing in the northern part of the Gulf is thought to be the reason for the year-round low surface temperatures in the vicinity of Ángel de la Guarda and Tiburón Islands, and for the relatively high temperatures, salinities, and oxygen concentrations at great depths in the isolated Delfín and Sal si Puedes Basins.

The water in the central and southern regions of the Gulf is in communication with the Pacific, and has the properties of Equatorial Pacific water. Below the thermocline the water is similar to that in the neighboring Equatorial Pacific with a salinity minimum of about 34.5‰ between 600 and 1000 m and a pronounced oxygen minimum of 0.1–0.2 ml/L between 400 and 800 m. Above the thermocline is a water mass referred to by Roden and Groves (1959) as "Gulf water." They view it as Equatorial Pacific water which has been transformed into water of higher salinity by evaporation.

The fish fauna indicates that the Gulf is clearly part of the Tropical American or Panamic faunal province. Walker (1960) in his review of the Gulf ichthyofauna, recorded 586 species of fish in the Gulf, of which 526 are shorefishes. Nearly ¾ of the shorefish are tropical or subtropical species with their principal ranges to the south of the Gulf. About 50 species, or 10% of the total, have their principal distributions to the north of the Gulf. The majority of these are found in the northern region of the Gulf, as disjunct species from the Southern California or San Diegan fauna. The remaining 92 species, or 17% of the total, are endemic to the Gulf.

In comparison with the Panamic fauna to the south, Walker has noted that the Gulf has an unusually high number of rocky shore species, a relatively poor representation of muddy bottom forms, and a high percentage of endemic species. The blennioid families Clinidae, Tripterygidae, and Chaenopsidae are perhaps the best examples of the profusion of rocky shore fishes in the Gulf. These groups have been reviewed extensively by a number of investigators including Hubbs (1952), Springer (1958), Rosenblatt (1959) and Steens (1963), and are among the best known of eastern Pacific shorefishes.

The high degree of speciation and endemism in these families might be accounted for by the abundance of semi-isolated rocky habitats, particularly on the peninsula coast of the Gulf. Also, the long stretch of sandy shoreline running from Guaymas to Mazatlán acts as a faunal barrier isolating the rocky shore fishes of the Gulf from those to the south. The paucity of muddy bottom species, most notably the

TABLE 1

Major constituents of three mid-water trawling expeditions to the Gulf of California

Species	Percent of Total Catch		
	Lavenberg and Fitch (1966)	Robison (1972)	Brewer (1973)
Myctophidae			
Triphoturus mexicanus	88.8	68.0	80.6
Diogenichthys laternatus	0.1	7.2	5.8
Benthosema panamense	5.0	2.8	0.9
Other myctophids	0.4	1.6	1.9
Gonostomatidae			
Vinciguerria lucetia	0.4	10.2	2.4
Cyclothone spp.	--	8.2	--
Bathylagidae			
Leuroglossus stilbius	0.5	0.6	5.4
Clupeidae			
Sardinops sagax caeruleus	1.6	--	--
Merlucciidae			
Merluccius sp.	1.3	--	--
Scombridae			
Scomber japonicus	0.6	--	--
All others	1.3	1.4	3.0

TABLE 2

Summary of occurrences and abundance (standard haul totals) of fish larvae in the Gulf of California during 6 cruises in 1956–1957

	5602		5604		5612		5702		5704		5706		Total	
Kinds of larvae	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.
Clupeidae:														
Sardinops sagax caeruleus	34	1,108	45	1,856	23	1,660	28	1,511	45	1,865	0	0	175	8,000
Etrumeus teres	11	122	40	1,090	12	335	11	172	24	757	10	278	108	2,754
Opisthonema spp.	0	0	0	0	0	0	0	0	0	0	55	23,217	55	23,217
Engraulidae	3	29	6	140	4	60	1	6	9	297	33	2,880	56	3,412
Bathylagidae:														
Bathylagus nigrigenys	8	57	6	85	2	13	3	27	8	123	13	90	40	395
Leuroglossus stilbius	50	1,139	42	1,217	14	209	32	2,168	27	357	1	6	166	5,096
Argentinidae:														
Argentina sialis	1	6	2	7	0	0	2	12	3	32	0	0	8	57
Gonostomatidae:														
Vinciguerria lucetia	35	4,718	37	4,278	32	1,800	38	18,218	34	6,818	87	19,231	263	55,063
Diplophos taenia	0	0	0	0	1	15	0	0	1	3	0	0	2	18
Sternoptychidae:														
Argyropelecus sp.	0	0	0	0	0	0	0	0	0	0	1	26	1	26
Stomiatidae:														
Stomias atriventer	1	3	2	20	0	0	1	15	1	6	6	43	11	87
Melanostomiatidae:														
Bathophilus filifer	0	0	0	0	3	22	0	0	3	19	0	0	6	41
Synodontidae:														
Synodus spp.	0	0	1	34	2	22	1	9	2	79	32	1,069	38	1,213
Aulopidae	0	0	0	0	0	0	0	0	0	0	1	4	1	4
Myctophidae:														
Benthosema panamense	12	115	0	0	36	1,438	0	0	2	148	56	5,685	106	7,386
Diaphus pacificus	0	0	0	0	4	187	0	0	1	12	2	13	7	212
Diogenichthys laternatus	45	2,142	45	2,301	32	1,342	41	2,178	29	2,326	49	2,451	241	12,740
Hygophum atratum	4	31	3	37	3	58	12	146	6	50	3	17	31	339
Lampanyctus spp.	8	103	9	103	6	45	1	10	7	62	13	140	44	463
Myctophum aurolaternatum	1	6	0	0	1	3	0	0	3	21	0	0	5	30
Triphoturus mexicanus	10	64	24	348	41	2,298	10	156	44	1,179	72	14,798	201	18,843
Myctophidae (unidentified)	2	18	0	0	5	71	2	26	3	34	18	290	30	439
Scopelarchidae:														
Scopelarchoides nicholsi	1	5	1	12	2	18	0	0	0	0	0	0	4	35
Paralepididae	0	0	0	0	2	12	0	0	0	0	2	6	4	18
Exocoetidae:														
(mostly *Oxyporhamphus*)	0	0	0	0	0	0	0	0	1	3	17	122	18	125
Gadidae:														
Merluccius sp.	5	35	19	460	0	0	4	24	9	67	0	0	37	586
Moridae:														
Physiculus spp.	5	27	3	172	2	20	6	49	1	6	0	0	17	274
Other	0	0	0	0	1	9	0	0	0	0	2	16	3	25
Macrouridae	0	0	5	47	2	21	2	19	2	11	0	0	11	98
Bregmacerotidae:														
Bregmaceros bathymaster	24	10,461	6	16,339	10	1,185	13	1,384	9	486	75	17,916	137	47,771
Fistulariidae	0	0	0	0	1	8	0	0	0	0	7	63	8	71
Syngnathidae	0	0	2	20	0	0	0	0	0	0	3	9	5	29
Melamphaidae	2	12	2	17	3	20	4	35	0	0	4	16	15	100
Leptocephali	6	29	5	42	11	102	7	66	16	115	44	263	89	617
Scombridae:														
Auxis sp.	0	0	1	13	1	3	1	2	2	27	60	1,789	65	1,834
Euthynnus	0	0	0	0	0	0	0	0	0	0	19	164	19	164
Sarda chiliensis	0	0	0	0	0	0	0	0	0	0	11	396	11	396
Scomber japonicus	34	6,469	64	2,891	7	100	29	2,969	50	4,008	4	17	188	16,454
Scomberomorus sp.	0	0	0	0	0	0	0	0	1	5	11	114	12	119
Unidentified	0	0	0	0	0	0	0	0	0	0	16	362	16	362
Apogonidae	0	0	0	0	1	5	0	0	0	0	2	7	3	12
Atherinidae	0	0	1	1	0	0	0	0	3	15	0	0	4	16
Bramidae	0	0	1	11	0	0	0	0	0	0	0	0	1	11
Branchiostegidae	0	0	0	0	0	0	0	0	2	15	2	14	4	29
Carangidae	2	17	13	90	17	281	3	21	6	36	56	1,317	97	1,762
Carapidae	1	3	1	3	1	40	1	17	1	5	7	56	12	124
Clinidae	0	0	0	0	0	0	0	0	3	38	0	0	3	38
Coryphaenidae	0	0	0	0	1	3	0	0	4	28	15	94	20	125
Gempylidae	0	0	0	0	2	5	0	0	0	0	0	0	2	5
Gerridae	0	0	0	0	0	0	0	0	0	0	27	2,064	27	2,064
Gobiidae	4	20	10	216	5	79	3	65	8	79	48	1,301	78	1,760
Kyphosidae	0	0	1	17	0	0	0	0	0	0	35	960	36	977
Labridae	1	6	0	0	0	0	1	129	1	7	16	95	19	237
Lutjanidae	0	0	0	0	0	0	0	0	0	0	2	6	2	6
Microdesmidae	0	0	0	0	0	0	0	0	0	0	3	11	3	11
Mugilidae	3	28	0	0	0	0	0	0	0	0	24	192	27	220
Nomeidae	0	0	0	0	9	149	0	0	8	93	42	415	59	657
Ophidiidae—Brotulidae	3	13	5	32	7	60	3	32	4	16	39	797	61	950
Polynemidae	0	0	0	0	0	0	0	0	0	0	6	141	6	141
Pomacentridae	9	153	0	0	0	0	0	0	1	2	15	218	25	373
Pomadasyidae	0	0	0	0	0	0	0	0	0	0	25	1,373	25	1,373
Sciaenidae	4	98	18	522	4	64	9	180	12	160	38	2,864	85	3,888

TABLE 2

Summary of occurrences and abundance (standard haul totals) of fish larvae in the Gulf of California during 6 cruises in 1956–1957 (Continued)

	5602		5604		5612		5702		5704		5706		Total	
Kinds of Larvae	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.	occ.	std. no.
Scorpaenidae:														
Sebastes spp.	8	75	15	87	5	101	6	174	1	6	0	0	35	443
Other	17	116	5	29	19	229	8	92	11	108	77	1,468	130	2,042
Serranidae	1	5	1	11	6	104	2	9	5	44	82	3,508	97	3,681
Sphyraenidae	0	0	0	0	0	0	0	0	1	4	15	136	16	140
Stromateidae	0	0	1	22	2	124	0	0	2	17	0	0	5	163
Tetragonuridae	0	0	0	0	2	20	0	0	0	0	0	0	2	20
Trichiuridae	4	37	1	13	12	232	2	32	1	5	28	4,668	48	4,987
Triglidae	2	18	4	41	4	23	2	21	12	166	38	510	62	779
Bothidae	9	76	48	620	31	536	15	145	22	138	141	2,746	264	4,261
Cynoglossidae:														
Symphurus	19	131	6	33	13	171	10	282	8	91	43	362	99	1,070
Balistidae	0	0	0	0	0	0	0	0	0	0	2	6	2	6
Tetraodontidae	0	0	0	0	0	0	0	0	0	0	4	35	4	35
Lophiidae	0	0	0	0	0	0	0	0	0	0	1	5	1	5
Gigantactinidae	0	0	0	0	0	0	0	0	1	6	0	0	1	6
Disintegrated	4	29	13	85	4	38	3	39	12	90	83	3,403	119	3,684
Unidentified	16	87	38	747	27	1,304	15	219	33	987	95	3,394	225	6,738
Total	93	27,611	129	34,109	79	14,644	70	30,659	125	21,072	132	123,657	628	251,752

croakers and catfishes, is more difficult to explain. Walker suggests that the wide expanse of open water across the mouth of the Gulf acts as a barrier isolating the Cape San Lucas region and lower peninsular coast from the mainland, but the general paucity of Panamic muddy and sandy bottom fishes in other areas of the Gulf probably relates to the lower temperatures and greater seasonal temperature ranges as compared to waters south of the Gulf. Certainly these are important limiting factors in the upper Gulf, which has only ½ the number of shore fish species found in the central and southern Gulf. Here also, the great tidal ranges probably also are a limiting factor.

The midwater fish fauna of the Gulf is reasonably well known, owing to recent studies by Lavenberg and Fitch (1966), Robison (1972), and Brewer (1973). Although their trawls differed in mouth size and in mesh size, essentially the same species were dominant in the three surveys (Table 1). As in midwater trawl surveys in other areas of the world, the family Myctophidae or lanternfishes dominated the three Gulf surveys, however, the dominance of these fishes was even more striking in the Gulf. They made up 94% of the catch in the Lavenberg and Fitch study, about 80% in Robison's samples, and 89% in Brewer's. A single myctophid species, *Triphoturus mexicanus*, was by all odds the dominant species; it represented 89%, 68% and 81% of all fish taken in the three surveys. As in the shorefishes, most of the midwater species of the Gulf have their principal distributions to the south of the Gulf, the notable exceptions being *T. mexicanus* and *Leuroglossus stilbius*, which are temperate-subtropical in distribution. To our knowledge there are no endemic midwater fishes in the Gulf, although several midwater fishes including *Hygophum atratum*, *L. stilbius* and *T. mexicanus* were described originally from the Gulf.

In general, the major midwater families are represented by a reduced number of species compared with waters at the same latitudes on the outer coast and adjacent waters south of the Gulf. For example, in the Myctophidae, about 30 species and 20 genera are found in outer coast waters and in adjacent waters to the south. Thirteen of these species and 10 of the genera, or less than half, are found in the Gulf. The same can be said for the Gonostomatidae, with about 10 species occurring on the outer coast and only 4 in the Gulf. Likewise, there are 5 species of bathylagid smelts in the outer coast waters and only 2 in the Gulf. A single species of the family Scopelarchidae has been taken in the Gulf whereas 5 species representing 4 genera are found on the outer coast. Typically, those midwater species recorded from the Gulf do not penetrate very far north and most are limited to the southernmost basins. Only *Vinciguerria lucetia*, *Diogenichthys laternatus*, *T. mexicanus*, and *L. stilbius* are widespread and abundant in the southern and central regions of the Gulf. *Benthosema panamense* and *T. mexicanus* are the only midwater species that occur in significant numbers in the upper regions of the Gulf.

Midwater trawls are highly selective sampling devices as shown by comparing their catches with relative abundances of species taken as larvae in plankton nets. The results of the CalCOFI cruises in the Gulf as shown below form an interesting comparison with those of the midwater trawl surveys.

RESULTS

Over a quarter of a million fish larvae (standard haul totals) were obtained on the six cruises. As shown in Table 2 the total numbers of larvae varied considerably from cruise to cruise. Cruise 5612 had the lowest total number of larvae, although on the basis of numbers of larvae per station, 5704 was the lowest with about 172 larvae per station. Cruise 5706 ranked highest in total numbers and in numbers per station with 937. Nearly as many larvae were collected on this single cruise as on the other five cruises combined.

In contrast to the fluctuation in numbers of larvae from cruise to cruise there was a general consistency in the kinds of larvae that were most abundant during the six cruises.

The larvae of two commercial species, the Pacific mackerel, *Scomber japonicus*, and the Pacific sardine, *Sardinops sagax caeruleus*, were highly prominent. Pacific mackerel larvae ranked second in total abundance on three of the six cruises (5602, 5702, 5704) and third on 5604 (Table 2). Overall they ranked fifth with 6.5% of the total larvae obtained on all six cruises (Table 3). They were widespread, as well as abundant, and on 5604 and 5704 had the highest number of occurrences of any species collected (Table 2). Spawning of *S. japonicus* (a species of northern affinity) was found to be curtailed sharply during the

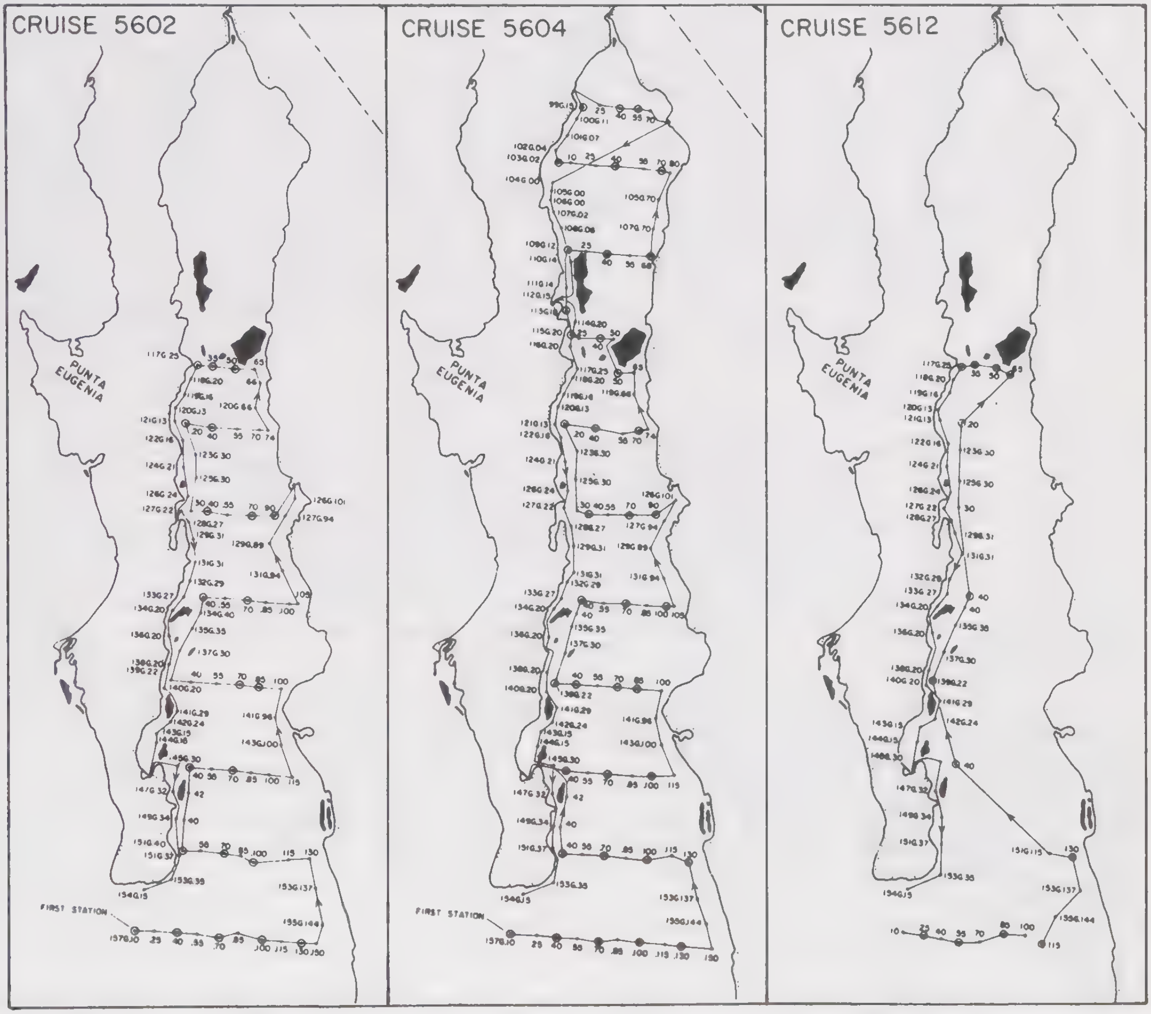

FIGURE 2. Station pattern for CalCOFI cruises into the Gulf of California in February, April, and December, 1956. From Oceanographic Observations of the Pacific: 1956 (SIO, 1963).

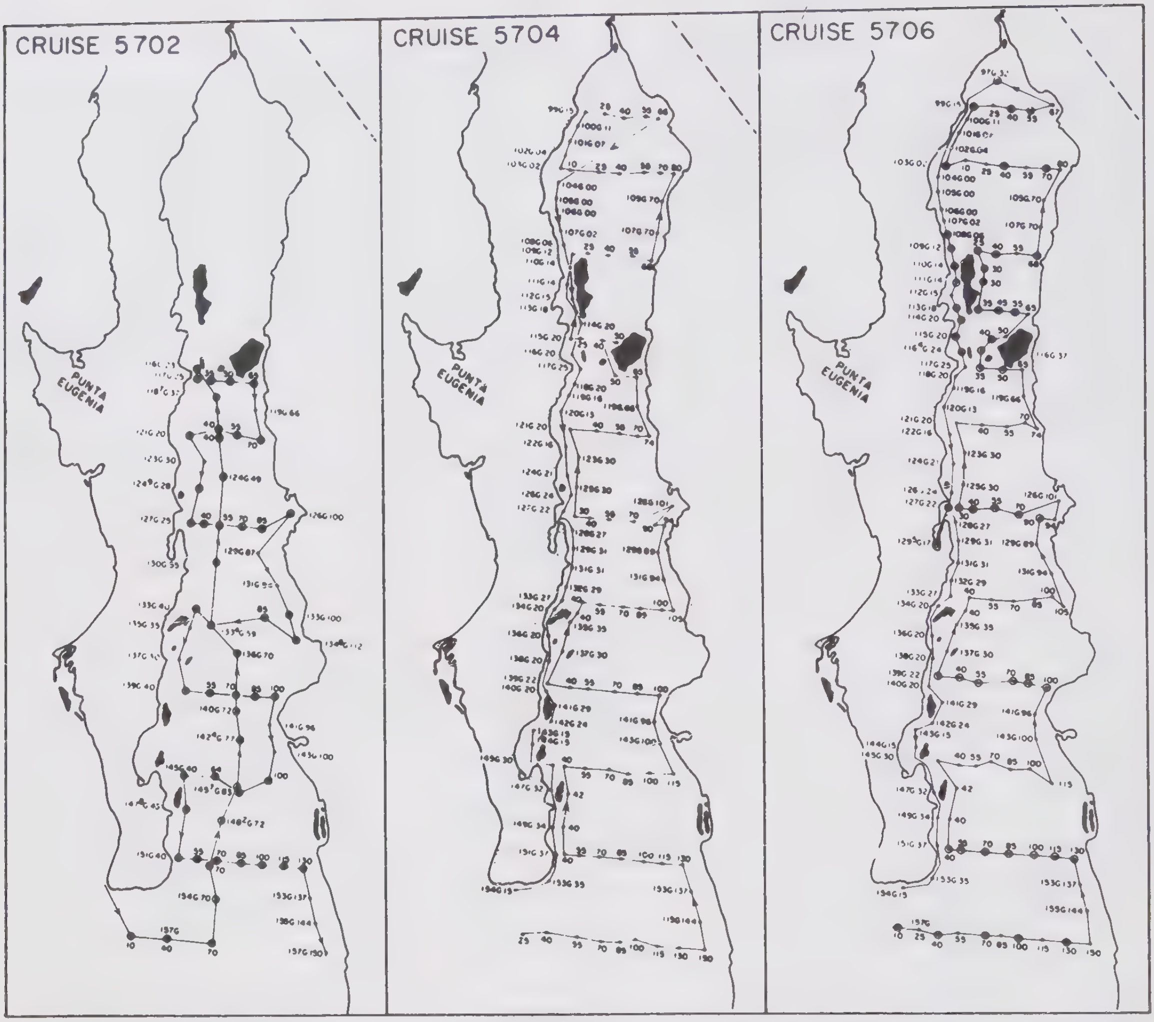

FIGURE 3. Station pattern for CalCOFI cruises into the Gulf of California in February, April, and June, 1957. From Oceanographic Observations of the Pacific: 1957 (SIO, 1965).

warm water cruise of 5706, and the larvae of tropical scombrids (*Auxis, Sarda, Euthynnus, Scomberomorus*) appeared in the collections.

Pacific sardine larvae were more consistent in relative abundance than those of Pacific mackerel, although they ranked as high as third on only one cruise (5612). They ranked sixth on 5602, fifth on 5604 and 5702, and fourth on 5704. It too is a species of cold water affinity and was not taken on 5706, but was replaced by larvae of the tropical clupeid genus *Opisthonema,* which ranked first in total abundance on that cruise.

Another species of potential commercial importance, the round herring, *Etrumeus teres,* was consistently represented on all but cruise 5706, it ranked no lower than eleventh and on two cruises, 5604 and 5704, ranked seventh.

The most consistently abundant species was the eastern Pacific lightfish, *Vinciguerria lucetia.* It ranked no lower than third in total abundance (5602), and on two cruises (5702, 5704), it ranked first. On 5702 it accounted for almost 60% of the total fish larvae collected. On 5706, it ranked second but occurred on 87 stations, the highest number of occurrences for any species during the six cruises. Its overall rank for all cruises was first, contributing 21.9% of all fish larvae obtained.

Another consistently abundant species was the small gadoid fish, *Bregmaceros bathymaster.* It was the most abundant species on the first two cruises, decreased in

TABLE 3

Rank and percentage contribution by cruise of categories of fish larvae that ranked among the top 25 for all cruises combined in Gulf of California during 1956–1957

Kinds of Larvae	5602		5604		5612		5702		5704		5706		Total	
	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%
Clupeidae:														
Sardinops sagax caeruleus	6	4.0	5	5.4	3	11.3	5	4.9	4	8.8	0	0	7	3.2
Etrumeus teres	10	0.4	7	3.2	9	2.3	11	0.6	7	3.6	--	0.2	17	1.1
Opisthonema spp.	0	0	0	0	0	0	0	0	0	0	1	18.8	3	9.2
Engraulidae	22	0.1	15	0.4	24	0.4	--	<0.1	10	1.4	10	2.3	16	1.4
Bathylagidae:														
Leuroglossus stilbius	5	4.1	6	3.6	13	1.4	4	7.1	9	1.7	--	<0.1	10	2.0
Gonostomatidae:														
Vinciguerria lucetia	3	17.1	2	12.5	2	12.3	1	59.4	1	32.4	2	15.5	1	21.9
Synodontidae:														
Synodus spp.	0	0	25	0.1	--	0.2	--	<0.1	21	0.4	20	0.9	24	0.5
Myctophidae:														
Benthosema panamense	11	0.4	0	0	4	9.8	0	0	13	0.7	5	4.6	8	2.9
Diogenichthys laternatus	4	7.8	4	6.8	5	9.2	3	7.1	3	11.0	13	2.0	6	5.1
Triphoturus mexicanus	16	0.2	12	1.0	1	15.7	12	0.5	5	5.6	4	12.0	4	7.5
Bregmacerotidae:														
Bregmaceros bathymaster	1	37.9	1	47.9	7	8.1	6	4.5	8	2.3	3	14.5	2	19.0
Scombridae:														
Auxis rochei	0	0	--	<0.1	--	<0.1	--	<0.1	--	<0.1	15	1.4	20	0.7
Scomber japonicus	2	23.4	3	8.5	21	0.7	2	9.7	2	19.0	--	<0.1	5	6.5
Carangidae	--	0.1	17	0.3	11	1.9	--	0.1	--	0.2	18	1.1	21	0.7
Gerridae	0	0	0	0	0	0	0	0	0	0	14	1.7	19	0.8
Gobiidae	--	0.1	13	0.6	22	0.5	18	0.2	22	0.4	19	1.0	22	0.7
Pomadasyidae	0	0	0	0	0	0	0	0	0	0	17	1.1	23	0.5
Sciaenidae	13	0.4	10	1.5	23	0.5	10	0.6	12	0.8	11	2.3	13	1.5
Scorpaenidae:														
(incl. *Sebastes*)	7	0.7	16	0.3	10	2.3	8	0.9	16	0.5	16	1.2	18	1.0
Serranidae	--	<0.1	--	<0.1	18	0.7	--	<0.1	--	0.2	7	2.8	14	1.5
Trichiuridae	18	0.1	--	<0.1	12	1.6	23	0.1	--	<0.1	6	3.8	11	2.0
Bothidae	15	0.3	9	1.8	8	3.7	13	0.5	14	0.7	12	2.2	12	1.7
Cynoglossidae:														
Symphurus spp.	9	0.5	--	0.1	15	1.2	7	0.9	19	0.4	--	0.3	25	0.4
Disintegrated specimens	23	0.1	19	0.2	--	0.3	20	0.1	20	0.4	8	2.8	15	1.5
Unidentified	14	0.3	8	2.2	6	8.9	9	0.7	6	4.7	9	2.7	9	2.7
All others	--	2.0	--	3.6	--	7.0	--	2.1	--	4.8	--	4.8	--	4.0

rank to seventh, sixth, and eighth during the next three cruises, and increased again to third on 5706. Its composite rank for all six cruises was second. Except for cruise 5706, this species was characterized by a relatively low number of occurrences. For example, on cruise 5604 it occurred on only six stations but accounted for nearly half the fish larvae taken on the entire cruise. Similarly clumped occurrences of this species were found on EASTROPAC cruises (Ahlstrom 1972).

Three species of lanternfishes of the family Myctophidae were abundant. The most consistent of these was *Diogenichthys laternatus* which ranked among the top five kinds of larvae in total abundance on all cruises except 5706, and ranked as high as third on two cruises (5702, 5704). It also had a consistently high number of occurrences, ranging from 29 in 5704 to 49 in 5706. For all cruises *D. laternatus* ranked sixth with 5.1% of the total larvae. Another lanternfish, *Triphoturus mexicanus,* ranked among the top ten on only three cruises, but on these it ranked first in abundance on 5612, fifth on 5704, and fourth on 5706. For all cruises *T. mexicanus* larvae ranked fourth with 7.5% of total fish larvae. *Benthosema panamense* ranked among the upper ten most abundant only on 5612 and 5706, but on these cruises ranked fourth and third, respectively. Its overall ranking was eighth.

Another midwater species, the deepsea smelt, *Leuroglossus stilbius,* was consistently abundant on five of the six cruises. It ranked fifth on 5602, sixth on 5604, thirteenth on 5612, fourth on 5702, and ninth on 5704. It also was characterized by a high number of occurrences, and on 5602 had the most occurrences (50) of any species collected. Being a species of northern affinity it occurred on only a single station on the warm water cruise of 5706. Its overall rank was tenth, with 2.0% of the total larvae.

It is interesting to compare the relative abundance of species of these cruises with the rankings for waters of the same latitudes on the outer coast. In 1956 (Table 4) the northern anchovy, *Engraulus mordax,* was by far the most abundant species, at about 38% of the total, followed by the hake, *Merluccius producuts,* with about 28%. These were followed by the sardine, *Sardinops sagax caeruleus,* and the genera *Sebastes* and *Citharichthys,* each of which made up about 4% of the catch. The lanternfish, *Triphoturus mexicanus,* and the tropical gonostomatid, *Vinciguerria lucetia,* ranked sixth and seventh at about 3% of the catch. In 1957, a warmer year, *E. mordax* remained the most abundant, but was followed closely by *V. lucetia*

TABLE 4

Relative abundance of fish larvae obtained on all CalCOFI cruises off the western coast of Baja California in 1956

Species	Rank	Standard No. of larvae	Percent of total	No. of occurrences
Engraulis mordax	1	116,464	37.6	363
Merluccius productus	2	87,708	28.3	281
Sardinops sagax caeruleus	3	13,975	4.5	149
Sebastes spp.	4	12,489	4.0	284
Citharichthys spp.	5	12,102	3.9	218
Triphoturus mexicanus	6	10,526	3.4	296
Vinciguerria lucetia	7	9,781	3.1	220
Leuroglossus stilbius	8	6,934	2.2	253
Trachurus symmetricus	9	5,907	1.9	156
Diogenichthys laternatus	10	3,123	1.1	115
Stenobrachius leucopsarus	11	2,009	0.6	98

TABLE 5

Relative abundance of fish larvae obtained on all CalCOFI cruises off the western coast of Baja California in 1957

Species	Rank	Standard No. of larvae	Percent of total	No. of occurrences
Engraulis mordax	1	66,502	26.0	376
Vinciguerria lucetia	2	54,369	21.2	546
Merluccius productus	3	46,298	18.1	227
Triphoturus mexicanus	4	15,308	5.9	578
Citharichthys spp.	5	14,224	5.5	326
Diogenichthys laternatus	6	11,581	4.5	398
Trachurus symmetricus	7	10,093	3.9	178
Sardinops sagax caeruleus	8	7,711	3.0	148
Leuroglossus stilbius	9	3,742	1.4	155
Stenobrachius leucopsarus	10	1,244	0.4	51
Sebastes spp.	11	1,014	0.3	227

TABLE 6

Relative abundance of fish larvae obtained on cruise 7203 of the Mexican research vessel ALEJANDRO DE HUMBOLDT in the Gulf of California

Kinds of Larvae	Rank	Standard No. of larvae	Percent of total	No. of occurrences
Merluccius spp.	1	4,301	56.6	17
Leuroglossus stilbius	2	716	9.4	9
Citharichthys spp.	3	709	9.3	14
Physiculus spp.	4	314	4.1	13
Etrumeus teres	5	253	3.3	12
Sardinops sagax caeruleus	6	205	2.7	10
Diogenichthys laternatus	7	205	2.7	5
Sebastes spp.	8	194	2.6	16
Unidentified	9	123	1.6	13
Scomber japonicus	10	76	1.0	5
Argentina sialis	11	74	1.0	5
Triglidae	12	74	1.0	8
Vinciguerria lucetia	13	54	0.7	4
Carangidae	14	42	0.6	2
Bregmaceros bathymaster	15	41	0.5	1
Stromateidae	16	37	0.5	2
Stomias atriventer	17	35	0.5	5
Scorpaenidae	18	32	0.4	4
Benthosema panamense	19	25	0.3	1
Symphurus spp.	20	25	0.3	1
Macrouridae	21	21	0.3	3
Disintegrated	22	19	0.2	4
Heterostomata	23	12	0.2	3
Sciaenidae	24	6	0.1	1
Triphoturus mexicanus	25	5	0.1	1
Leptocephali	26	3	<0.1	1

(Table 5). The hake remained abundant, in third place, followed by *T. mexicanus*, *Citharichtys* spp., and the warm-water lanternfish, *Diogenichthys laternatus*.

It is also useful to compare the relative abundance of species of the Gulf cruises of 1956 and 1957, with those of a recent cruise in a restricted area of the northern Gulf (Table 6). In March 1972 the Mexico/FAO/UNDP Fisheries Research and Development Program research vessel, ALEJANDRO DE HUMBOLDT, occupied 28 stations, largely in the cold water region around Ángel de la Guarda and Tiburón Islands. The hake, *Merluccius* sp., made up over half of the the total followed by *Leuroglossus stilbius* and *Citharichthys* spp. at about 9% of the total. The gadoid genus, *Physiculus*, ranked 4th at about 4%, followed by *Etrumeus teres*, *Diogenichthys laternatus*, and *Sardinops sagax caeruleus* each at about 3%. It is apparent that the rankings from this cruise in a restricted area of cold water in the northern Gulf correlate more closely with the rankings for the outer coast waters during 1956 and 1957 than with those within the Gulf for those years.

The seasonal fluctuations in areal distribution of fish larvae within the Gulf are shown in Figures 4–24.

Larvae of the Pacific mackerel, *Scomber japonicus*, were widespread in the southern region of the Gulf during the February cruises of both years (Figures 4, 5). Abundance tended to diminish towards the north and their distribution terminated well south of Tiburon Island. In the April cruises, *S. japonicus* larvae were widespread and abundant throughout all regions of the Gulf with some regions of coastal concentration and with a marked absence at the cold water region around the large islands of the upper Gulf. The lower abundance toward the north on the February

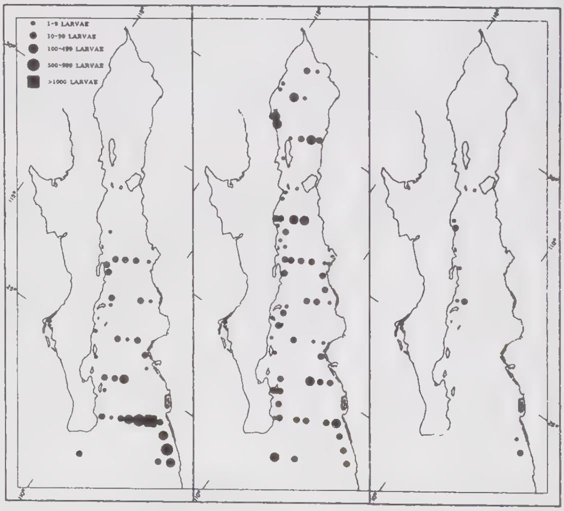

FIGURE 4. Distribution and abundance of *Scomber japonicus* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

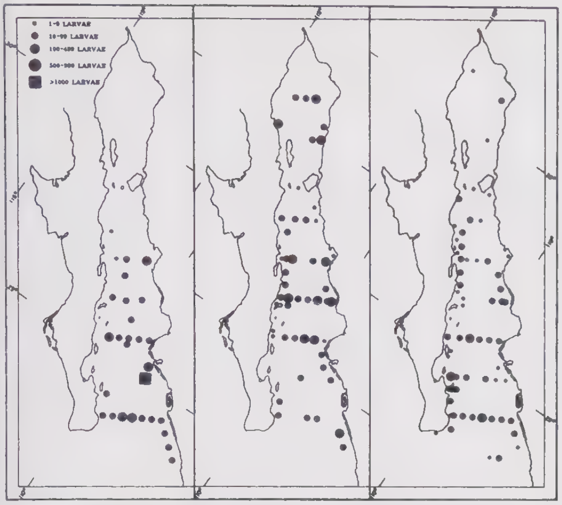

FIGURE 5. Distribution and abundance of *Scomber japonicus* larvae on CalCOFI cruises 5702 (left) and 5704 (center) and *Auxis rochei* larvae on cruise 5706 (right) in the Gulf of California.

cruises suggests a progression of spawning related to rising surface temperatures.

Larvae of *S. japonicus* were strikingly more abundant and widespread in the Gulf than on the outer coast, where they averaged about three larvae per station during the spawning seasons of 1956 and 1957. In the Gulf the average for the February and April cruises was about 39 larvae per station.

The abundance of *S. japonicus* in the Gulf is even more apparent from egg abundance, which was over 3,000 per station in some areas of the Gulf (Figure 6).

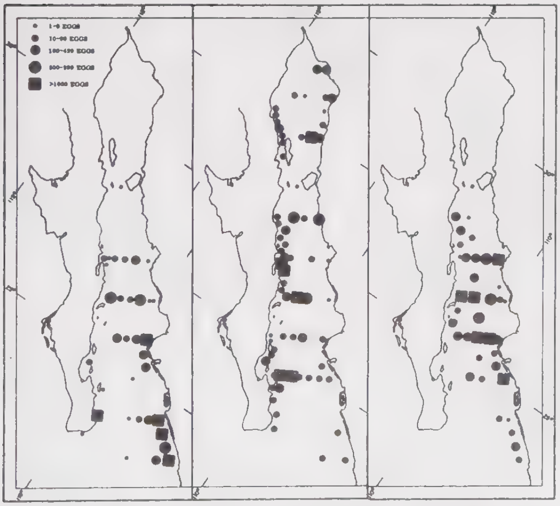

FIGURE 6. Distribution and abundance of *Scomber japonicus* eggs in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5702 (right).

The widespread nature of spawning in 5604 is shown in the chart, as is the avoidance of the cold water region around the large islands. Approximate calculation of spawning stock size from egg abundance, using the method of Ahlstrom (1968), gives a conservative estimate of about 500,000 metric tons for 5602 and about 300,000 tons for 5604 and 5702. This is at least five times the estimate for the spawning stock on the outer coast during the same years.

Concomitant with the marked scarcity of *S. japonicus* larvae on cruise 5706, the larvae of other scombrids made their appearance. Larvae of the bullet mackerel, *Auxis rochei,* were abundant and widely distributed in the central and southern Gulf and occurred on a few stations in the upper region (Figure 5). Larvae of the black skipjack, *Euthynnus lineatus,* occurred in the southern region but were fewer in the central region and did not occur in the north (Figure 7). The larvae of the bonito, *Sarda chiliensis,* and the sierra, *Scomberomorus* spp., showed a nearly opposite distribution with a small area of high concentration along the western coast of the upper Gulf and only a few occurrences to the south (Figure 7).

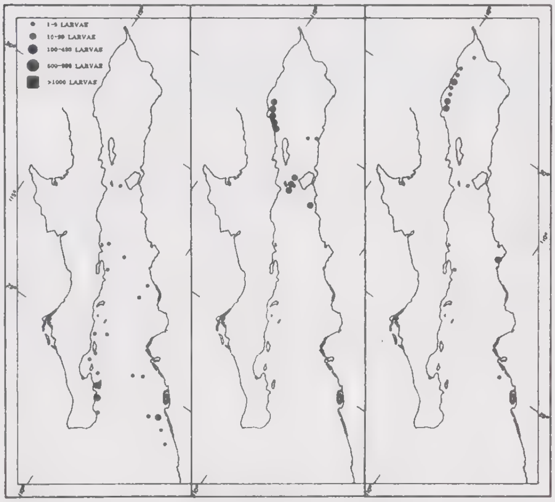

FIGURE 7. Distribution and abundance of larvae of *Euthynnus lineatus* (left), *Sarda chiliensis* (center) and *Scomberomorus* spp. (right) on CalCOFI cruise 5706 in the Gulf of California.

The sardine, *Sardinops sagax caeruleus,* is a species of northern affinity, occurring from British Columbia to the Cape San Lucas region. On the February cruises (Figures 8, 9) its larvae were widespread and abundant in the central region and diminished to the north and south. In the April cruises larvae occurred widely in the upper Gulf but remained most abundant in the central region of the Gulf. The eggs showed a patchy and more restricted distribution, with high numbers in the central portion of the Gulf and isolated patches in the northern and southern regions (Figure 10). Calculation of spawning stock size from egg abundance gives an estimate of about 48,000, 505,000 and

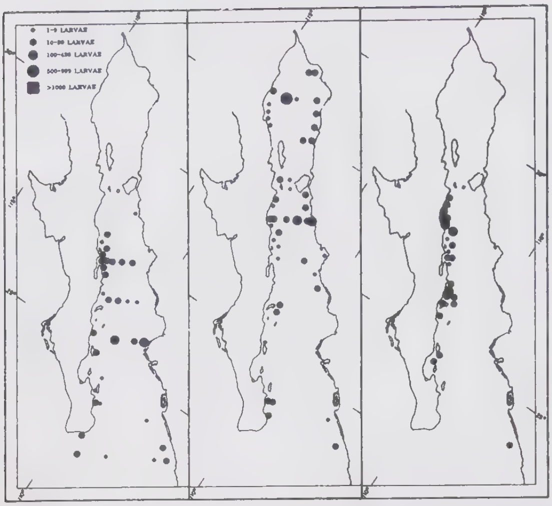
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 8. Distribution and abundance of *Sardinops sagax caeruleus* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

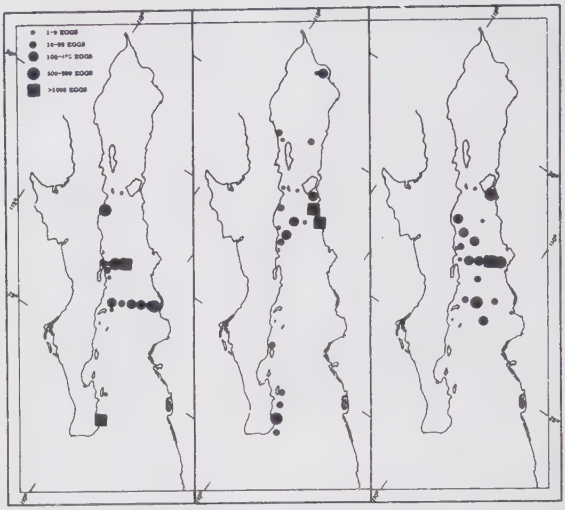
1-9 EGGS
10-99 EGGS
100-499 EGGS
500-999 EGGS
>1000 EGGS

FIGURE 10. Distribution and abundance of *Sardinops sagax caeruleus* eggs in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5702 (right).

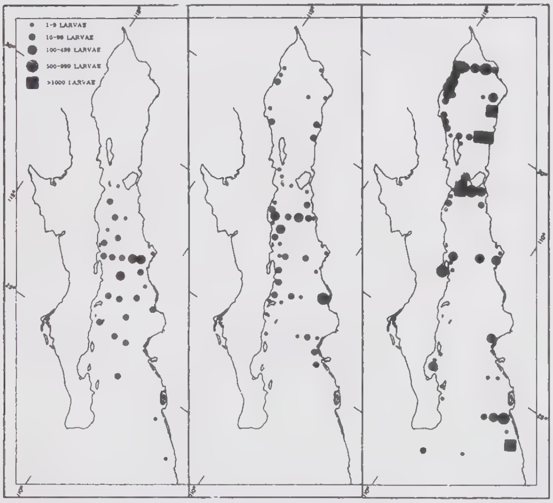
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 9. Distribution and abundance of *Sardinops sagax caeruleus* larvae on CalCOFI cruises 5702 (left) and 5704 (center) and larvae of *Opisthonema* spp. on cruise 5706 (right) in the Gulf of California.

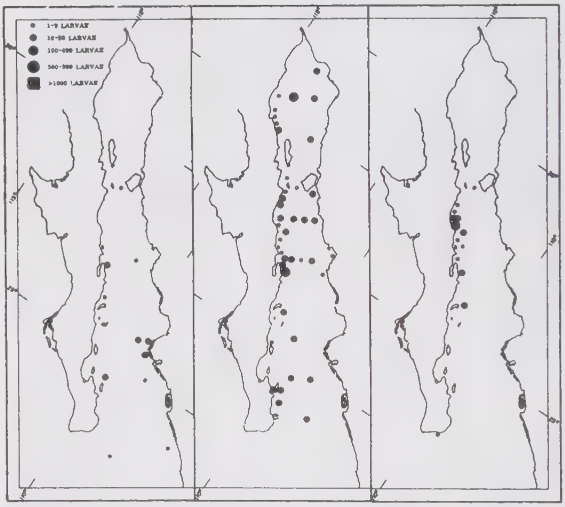
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 11. Distribution and abundance of *Etrumeus teres* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

74,000 metric tons for 5602, 5604, and 5702 respectively.

As with other species of northern affinity, the larvae of the sardine were not present during the June cruise. This void was filled by the larvae of the tropical clupeid genus, *Opisthonema* (Figure 9). The larvae were patchily distributed throughout the Gulf with pockets of high concentration in coastal areas, and even in Bahía Concepción.

Larvae of the round herring, *Etrumeus teres,* had a seasonal fluctuation in abundance (Figures 11, 12). They occurred scantily in the southern and central regions during February. In April of 1956 they were widespread and abundant throughout the entire Gulf but in 5704 they were only abundant in the upper and central regions and were almost absent in the southern region. In 5706 they occurred only in the upper Gulf and on two stations in the vicinity of La Paz.

Vinciguerria lucetia has the typical distributional pattern for tropical midwater species in the Gulf—decreasing abundance from south to north (Figures

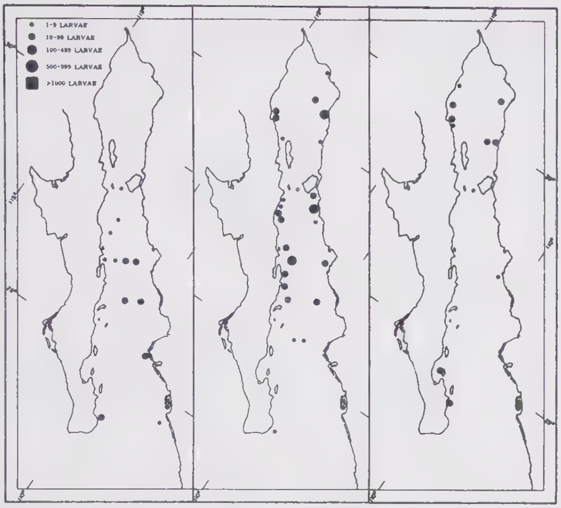
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 12. Distribution and abundance of *Etrumeus teres* larvae in the Gulf of California on CalCOFI cruises 5702 (left), 5704 (center) and 5706 (right).

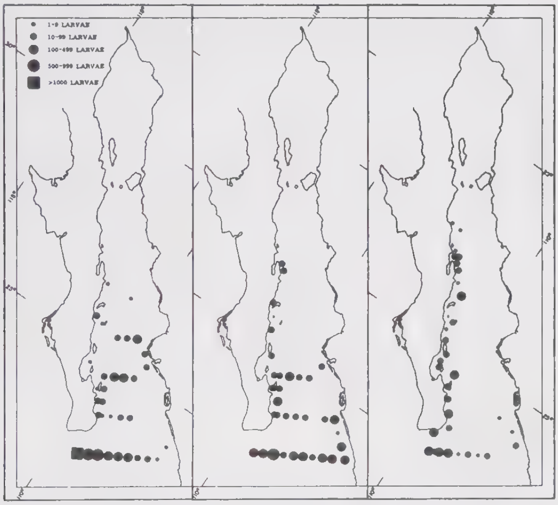
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 13. Distribution and abundance of *Vinciguerria lucetia* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

13, 14). In five of the six cruises shown, this species was widespread and abundant in the southern Gulf, scattered and much less abundant in the central Gulf, and absent from the upper portion. Only in 5706 did the larvae appear in abundance as far north as Tiburón Island. Here also there was a single record in the upper Gulf. Within its latitudinal range in the Gulf, *V. lucetia,* like other abundant midwater species, tends to be more concentrated over the deep waters of the central and western side of the Gulf, compared with the shallower waters of the eastern side.

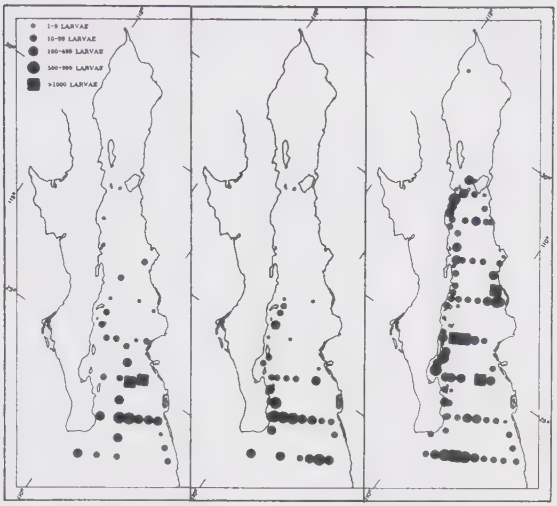
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 14. Distribution and abundance of *Vinciguerria lucetia* larvae in the Gulf of California on CalCOFI cruises 5702 (left), 5704 (center) and 5706 (right).

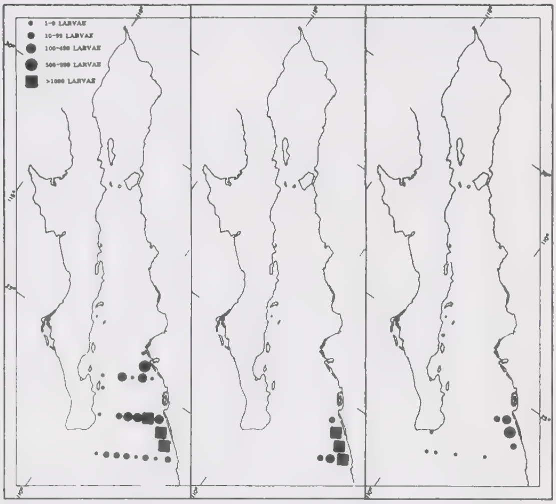
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 15. Distribution and abundance of *Bregmaceros bathymaster* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

Larvae of *Bregmaceros bathymaster* had a highly concentrated and restricted distribution at the southern end of the Gulf on five of the six cruises (Figures 15, 16). On 5706 the larvae were widespread and abundant as far north as Tiburón Island. On all these cruises it is evident that the species is concentrated near shore and shows a general diminution over open water areas of the Gulf. This is consistent with Ahlstrom's (1971, 1972) findings that *B. bathymaster* is a coastal species in the eastern tropical Pacific.

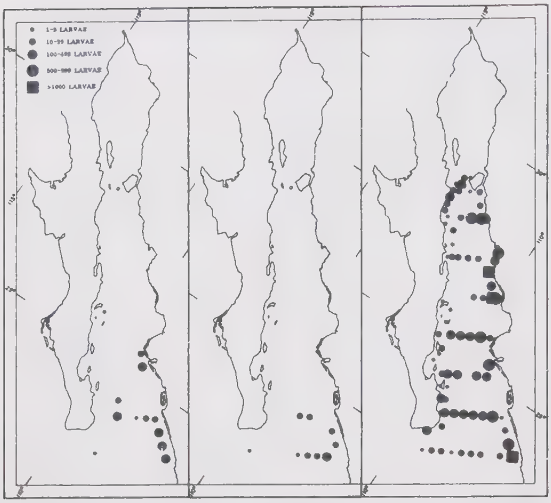
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 16. Distribution and abundance of *Bregmaceros bathymaster* larvae in the Gulf of California on CalCOFI cruises 5702 (left), 5704 (center) and 5706 (right).

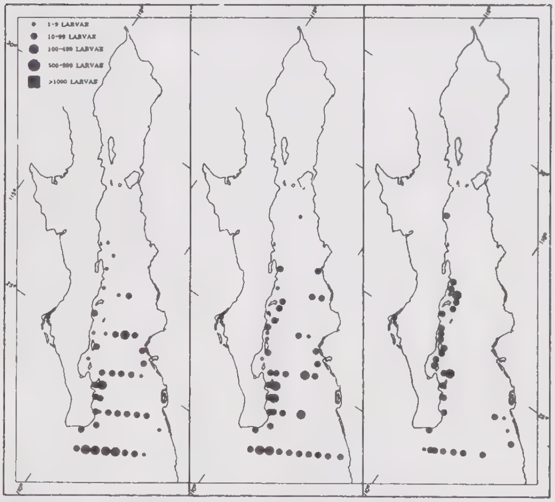
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 17. Distribution and abundance of *Diogenichthys laternatus* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

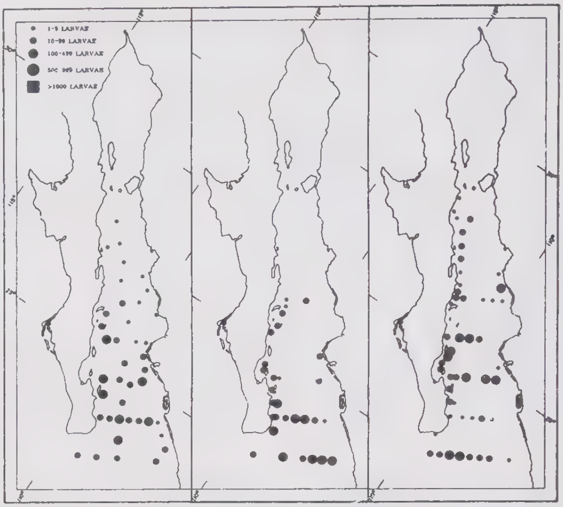
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 18. Distribution and abundance of *Diogenichthys laternatus* larvae in the Gulf of California on CalCOFI cruises 5702 (left), 5704 (center) and 5706 (right).

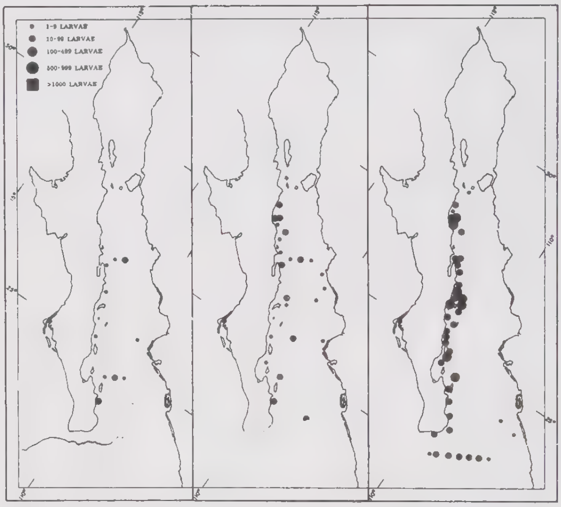
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 19. Distribution and abundance of *Triphoturus mexicanus* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

The lanternfish, *Diogenichthys laternatus,* has a distribution similar to that of *Vinciguerria* (Figures 17, 18). It is widespread and abundant in the southern region, diminishes markedly in abundance in the central region, and is totally absent from the upper Gulf. Like *Vinciguerria* it tends to be more abundant in the center and along the western side of the Gulf, generally avoiding the shallow areas of the eastern side.

The lanternfish, *Triphoturus mexicanus,* showed a marked seasonal abundance (Figures 19, 20). On the two February cruises, larvae were scarce and were restricted to the central and southern regions of the Gulf. Larvae were abundant and widespread on the two April cruises but remained restricted to the central and southern regions. The tendency for larvae to be concentrated along the western side of the Gulf and to diminish in density towards the east and near the mouth of the Gulf is beginning to be evident on these cruises. This tendency is strikingly illustrated on 5706, where abundance has increased markedly and some larvae occurred in the upper Gulf. It is obvious that the center of distribution of *T. mexicanus* in the

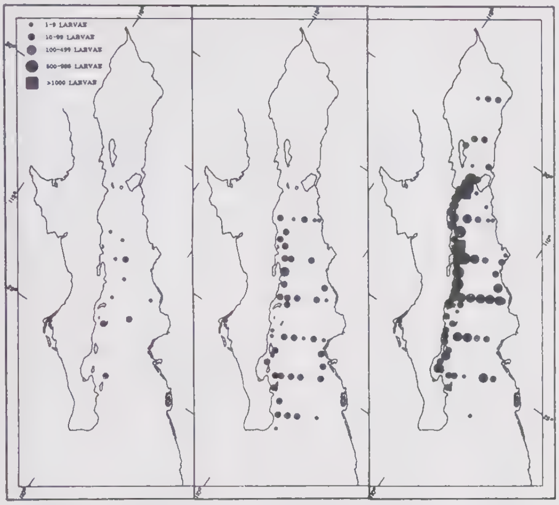
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 20. Distribution and abundance of *Triphoturus mexicanus* larvae in the Gulf of California on CalCOFI cruises 5702 (left), 5704 (center) and 5706 (right).

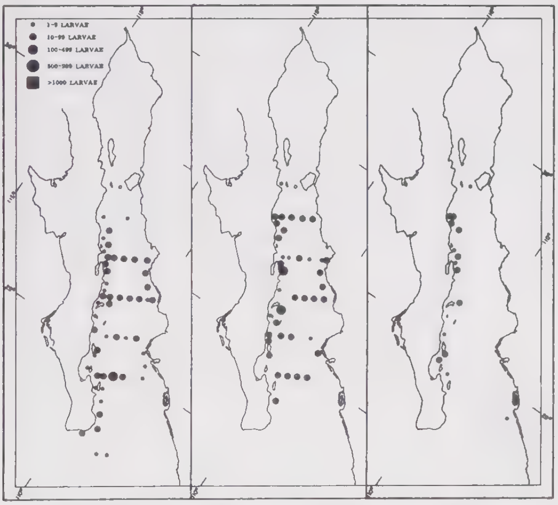
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 21. Distribution and abundance of *Leuroglossus stilbius* larvae in the Gulf of California on CalCOFI cruises 5602 (left), 5604 (center) and 5612 (right).

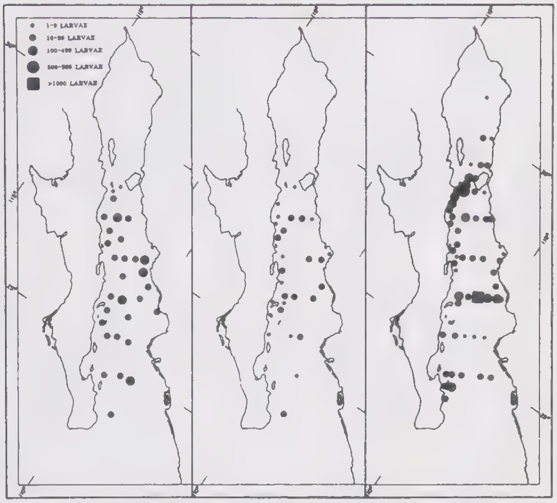
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 22. Distribution and abundance of *Leuroglossus stilbius* larvae on CalCOFI cruises 5702 (left) and 5704 (center) and *Benthosema panamense* larvae on cruise 5706 (right) in the Gulf of California.

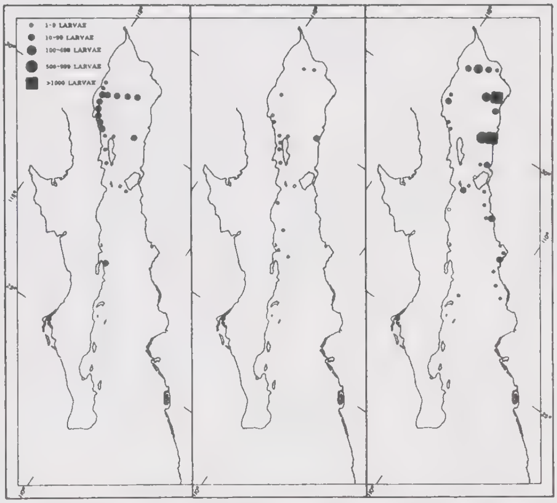
1-9 LARVAE
10-99 LARVAE
100-499 LARVAE
500-999 LARVAE
>1000 LARVAE

FIGURE 23. Distribution and abundance of larvae of *Merluccius* sp. on CalCOFI cruise 5604 (left), larvae of *Sebastes* spp. on cruise 5604 (center) and *Trichiurus nitens* larvae on cruise 5706 (right) in the Gulf of California.

Gulf is in the central region along the islands of the western coast. A very similar pattern of distribution is shown for the myctophid, *Benthosema panamense* (Figure 22).

The deep sea smelt, *Leuroglossus stilbius,* is essentially a cold water species that ranges from Cape San Lucas to the Gulf of Alaska. It has a distributional pattern that is somewhat similar to that of *T. mexicanus* although spawning occurs more evenly throughout the cold months of the year (Figures 21, 22). Larvae were abundant and widely distributed throughout the central region of the Gulf during February and April but their northward distribution terminated abruptly at Tiburón Island and more gradually southward towards the mouth. Within its latitudinal range in the Gulf, *L. stilbius* is evenly distributed and does not appear to concentrate along the western side like *T. mexicanus.*

Larvae of the genus *Sebastes* are definitely cold water fishes, and the restriction of their larvae to the cold water region around the large islands in the

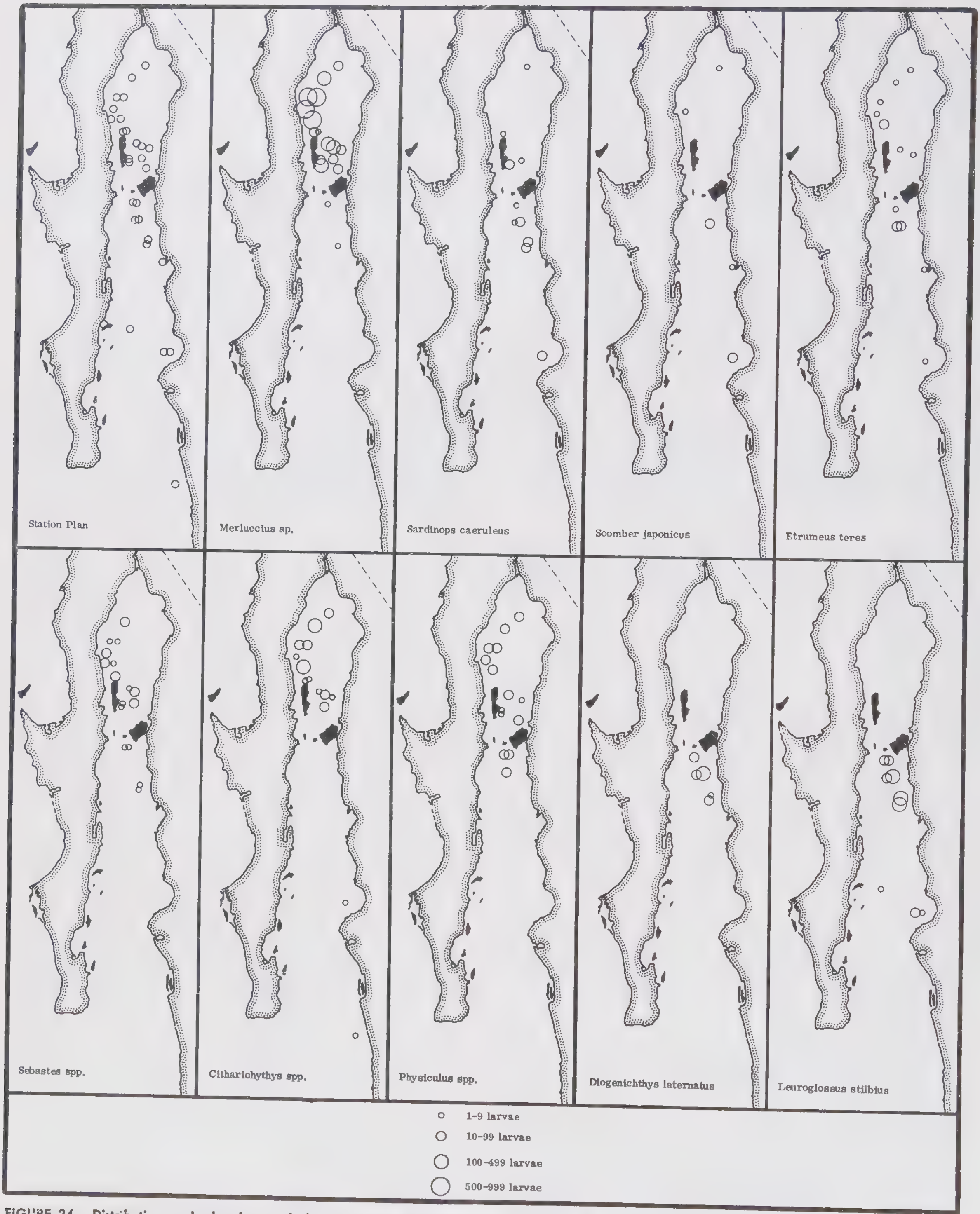
Station Plan
Merluccius sp.
Sardinops caeruleus
Scomber japonicus
Etrumeus teres
Sebastes spp.
Citharichthys spp.
Physiculus spp.
Diogenichthys laternatus
Leuroglossus stilbius
○ 1-9 larvae
○ 10-99 larvae
○ 100-499 larvae
○ 500-999 larvae

FIGURE 24. Distribution and abundance of the nine most abundant larvae obtained on cruise 7203 (March, 1972) of the Mexico/FAO/UNDP Fisheries Research and Development Program in the Gulf of California.

upper Gulf is shown in Figure 23. The larvae of the hake, *Merluccius* sp., have a similar distribution in the vicinity of these islands (Figure 23). According to Dr. Mathews (see this symposium) these larvae are of an endemic species which occurs southward as far as Bahía Concepción. The larvae of the cutlassfish, *Trichiurus nitens,* has an interesting distribution (Figure 23). It is abundant along the eastern coast of the upper Gulf and is scantily distributed along the eastern coast in the central region of the Gulf.

Areal distributions and abundances of larvae from the cruise of the ALEJANDRO HUMBOLDT in March of 1972 are shown in Figure 24. Although the pattern of stations was largely concentrated in the vicinity of the large islands in the upper Gulf, the larval distributions correlate closely with those shown by the more extensive CalCOFI cruises. The hake, *Merluccius* sp., was extremely abundant near and to the north of the island. The three epipelagic species, *Sardinops sagax caeruleus*, *Scomber japonicus*, and *Etrumeus teres,* were move evenly distributed throughout the station pattern. The rockfishes, *Sebastes* spp., had a distribution similar to *Merluccius*, as did the larvae of the gadoid genus *Physiculus*. The two midwater species, *Leuroglossus stilbius* and *Diogenichthys laternatus*, were restricted to south of Tiburón Island.

DISCUSSION

The Gulf of California offers a paradoxical environment for those organisms that would invade its waters and flourish. On one hand it has some of the greatest environmental extremes of any of the world's seas. With a seasonal surface temperature flux that increases from 9° C at the mouth to as high as 22° C at the head, it offers the most extreme annual temperature range of any region in the eastern Pacific. An evaporation basin, its surface salinities are typically 1–2‰ higher than waters of the outer coast and increase 1–2‰ from the mouth to the head of the Gulf. The extreme tidal ranges of the upper Gulf, as great as 10 m, are well known. Equally well known is the pronounced oxygen minimum of 0.1–0.2 ml/L at 400–800 m depth in the central and southern Gulf.

Counterposed against these conditions is the great productivity of the Gulf. Prevailing northerly winds during the winter months induce upwelling in the lee of islands and capes along the eastern coast, while during summer months, the prevailing southerly winds cause upwelling along the peninsular coast. Tidal currents around the large islands of the upper Gulf insure a continual vertical mixing of water in that region. The result of this widespread upwelling of nutrient-rich water is an enormous productivity. The year-round plankton blooms are a notable feature of the Gulf and provoked the early explorer, Ulloa, to name it the "Vermillion Sea" (van Andel, 1964). Such productivity, with its attendant abundance of life at higher levels of the food web would seem to assure a propitious environment for those fish species capable of meeting the environmental demands outlined above. That the harsh environmental factors reduce the attractiveness of this environment is obvious from an examination of the ichthyofauna.

The depauperate nature of the shorefish fauna has been described by Hubbs (1960), Hubbs and Roden (1964) and Walker (1960). Isolated from the effects of the cold California Current, except in the area of Cabo San Lucas, the elevated water temperatures have allowed Panamic shorefishes to dominate the Gulf and extend considerably northward of their limits on the outer coast. The paucity of certain Panamic groups (croakers, catfishes, and anchovies) indicates their inability to adapt to the environmental extremes of the Gulf. In contrast, these extremes, along with the abundance and isolated nature of rocky shore habitats have allowed an impressive evolution of blennioid fishes.

The midwater fish fauna, also dominated by warm water species, is even more depauperate than the shorefish fauna (Lavenberg and Fitch, 1966; Robison, 1972, Brewer, 1973). These investigators have established that only a few midwater species are abundant and that most of midwater species recorded for the Gulf are restricted to the southern portion. This is even more graphically shown by the data on larvae presented herein. The larvae of only six mesopelagic species were abundant. The gonostomatid, *Vinicguerria lucetia,* ranked first among all species recorded and represented 22% of all the fish larvae obtained in the six cruises. Striking in their total absence were the larvae of the gonostomatid genus, *Cyclothone,* which are extremely abundant in waters adjacent to the Gulf. Less abundant than *V. lucetia* but prominent on certain cruises were the myctophids, *Benthosema panamense*, *Diogenichthys laternatus*, and *Triphoturus mexicanus* and the bathylagid smelt, *Leuroglossus stilbius*. The gadoid, *Bregmaceros bathymaster,* was abundant on all cruises and ranked second in overall abundance with 19% of all larvae obtained on the six cruises. Only a few adults of *B. bathymaster* were recorded from the three midwater trawling expeditions, indicating that plankton hauls obtain a much more representative sampling of a fauna than do midwater trawls.

Except for *T. mexicanus* and *B. panamense,* which occurred sparsely in the upper Gulf on cruise 5706, the larvae of the abundant midwater species were restricted to the central and southern Gulf. The proclivity of these species for waters of the western side of the Gulf is strikingly illustrated by the distribution of *T. mexicanus* larvae on cruise 5706. Larval abundance of the warm water species, *V. lucetia, B. panamense, D. laternatus, T. mexicanus,* and *B. bathymaster,* increased with rising water temperatures and were most abundant on cruise 5706. Also, the areal extent of spawning increased northward with rising water temperatures. This is best illustrated by *B. bathymaster* larvae which were restricted to the extreme southern Gulf from December to April but were abundant and widespread northward to Tiburon Island in June of 1957. Larvae of the bathylagid smelt, *L. stilbius,* of northern affinity, showed an opposite pattern of seasonal abundance. They were abundant and widespread during the cold months and all but absent on the June cruise.

The larval distributions clearly show that the abundant midwater species of the Gulf are restricted areally and in season of reproduction. Why these few species should be able to flourish in the Gulf, while the members of the rich midwater fauna of adjacent waters are excluded is of great interest. All of the abundant Gulf species have wide latitudinal ranges outside the Gulf and are equipped to tolerate the seasonal temperature range of the Gulf. Probably more important than this is their ability to tolerate the low oxygen concentrations at 400–800 m depth. The effect of this oxygen-poor zone is certainly obvious where it impinges on the coast, as Parker (1964) has shown that these areas are all but devoid of animal life. Also suggestive of the importance of the oxygen minimum zone is the fact that *Scopelarchoides nicholsi*, the sole scopelarchid recorded from the Gulf, has the greatest development of gill filaments of any member of that family (Johnson, 1971). The vertical distributions of most of the abundant midwater species of the Gulf are shoaler than 400 m (Robison, 1972) thus they have adapted to the oxygen minimum zone by simply avoiding it. The exception, *T. mexicanus*, whose daytime depths overlap broadly with the oxygen minimum zone, may adapt behaviorly by becoming lethargic as suggested by Barham (1970).

The epipelagic species of commercial importance are largely unaffected by the oxygen minimum layer. The larval data shows that two species of northern affinity, *Scomber japonicus* and *Sardinops sagax caeruleus*, are strikingly abundant throughout the Gulf. These species have broad latitudinal ranges outside of the Gulf and are well suited to tolerate the Gulf's annual temperature extremes. Spawning of these species is restricted to the cold water months as illustrated by the near absence of their larvae in the June cruise. During warm water months *Sardinops* larvae are replaced by those of the warm water Clupeid genus, *Opisthonema,* which appears to be heavily concentrated in the upper Gulf. The data suggests that these thread herring may be the most abundant pelagic fishes in the Gulf since their larvae represented 9 percent of the total fish larvae even though a fraction of their probable spawning season was sampled. The larvae of *Scomber* are replaced by those of the more tropical scombrids *Auxis, Euthynnus, Sarda* and *Scomberomorus.* Of these, *Auxis* larvae are the most widespread and abundant, although the restricted distributions of the others may simply reflect the partial sampling of their spawning seasons.

The data from the recent plankton tows of the ALEJANDRO DE HUMBOLDT in March 1972 indicate that the demersal hake, *Merluccius* sp., is an extremely abundant fish in the upper Gulf, particularly in the areas just east and north of Angel de la Guarda Island. This abundance was not apparent from the data of the CalCOFI cruises, since only on cruise 5604 were significant numbers of larvae taken. A possible explanation for this is that the reproductive season of the species is very short. It may reach its peak in March, as suggested by the data from cruise 7203, and may last only a month. This could explain the poor representation of *Merluccius* larvae in the CalCOFI samples of February and April. Such an abbreviated reproductive season, limited to the coldest time of the year, is also typical of *Sebastes* and other pleistocene relicts of the upper Gulf.

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Distributional Ecology and Behavioral Thermoregulation of Fishes in Relation to Heated Effluent from a Power Plant at Lake Monona, Wisconsin

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ABSTRACT

Cooling water for a 220-megawatt power plant is pumped from 5 m beneath Lake Monona's surface, heated about 10 C, and discharged into the littoral zone. Maximum temperatures in the effluent-outfall area approach 35 C in summer and 14 C in winter; unheated parts of the littoral zone rarely exceed 29 C.

To assess distributional responses of fishes to operation of the power plant, the outfall area and two reference areas were electrofished on 30 dates between 8 August 1968 and 21 August 1969. Some fishes avoided the outfall area; these were *Perca flavescens*, *Cottus bairdi*, subadult *Morone mississippiensis*, and subadult *Ictalurus melas*. Others were occasionally or usually concentrated in the outfall area relative to reference areas—*Lepisosteus osseus*, adult *Cyprinus carpio*, adult *M. mississippiensis*, young *Lepomis gibbosus*, *L. macrochirus*, and *Micropterus salmoides*. The tendency for fish of a given species and size to concentrate in or avoid the outfall area generally did not reverse from season to season or from day to night.

Any differences in growth rate of young fishes among outfall and reference areas were obscured by size-dependent movements of the fish.

In August 1970, body temperature of fishes in the outfall area varied with species and time of day. During afternoon, median temperatures of *Cyprinus carpio*, *Lepomis gibbosus*, *L. macrochirus*, and *Micropterus salmoides* were higher than 29 C, while those of *Morone mississippiensis*, *Ambloplites rupestris*, *Pomoxis nigromaculatus*, and *Perca flavescens* were lower than 29 C. At night, only *Lepisosteus osseus* and *C. carpio* had median body temperatures higher than 29 C.

Young *Lepomis macrochirus* collected during summer 1970 from the outfall area had estimated acclimation temperatures between 29.4 and 31.3 C, even though temperatures between 25 and 36 C were available. To have had acclimations between 29.4 and 31.3 C, the fish must have avoided exposure to temperatures higher than about 31.5 C. This conclusion agreed substantially with the distribution of body temperatures of young *L. macrochirus*; the highest body temperature among 31 specimens was 31.8 C.

Temperatures at which fishes lived in the outfall area during summer 1970 were positively correlated ($p < 0.01$) with the degree to which they were concentrated in the outfall area during the two previous summers. The strength of the correlation argued that, during summer, temperature was the primary factor governing not only distribution of fishes within the outfall area, but also the abundances of fishes in the outfall area relative to unheated parts of the littoral zone.

Moreover, integration of field and laboratory results suggested that fishes were distributed within the outfall area according to their different temperature preferenda. Preferred temperatures of six Lake Monona fishes were measured by allowing each of several specimens to behaviorally regulate the temperature of its tank. Midpoint of the preferred temperature range agreed well with the median body temperature recorded in the outfall area during afternoon (considering, in the case of *Perca flavescens*, that temperatures below 26.5 C were not available in the outfall area): *Cyprinus carpio*, 31.8 C (laboratory), 30.6 C (field); *Lepomis macrochirus*, 30.3, 29.4; *Micropterus salmoides*, 29.1, 29.7; *Pomoxis nigromaculatus*, 28.3, 28.3; *A. rupestris*, 27.3, 27.5; and *Perca flavescens*, 23.4, 27.1.

In other laboratory experiments, *Lepomis macrochirus* and *Perca flavescens* were required to partition time between an environment with preferred temperature and an environment with food but either warmer or cooler than the preferred temperature. Each species made forays for food into water with extreme temperatures. However, neither laboratory nor field results suggested that thermoregulatory behavior was overridden by feeding behavior, even though zooplanktonic food was more abundant in the outfall area than in unheated parts of the littoral zone.

INTRODUCTION

Rapid expansion of the steam-electric power industry has spurred concern for the potential impact of thermal effluents on aquatic ecosystems. As much as one-fifth of the total freshwater runoff in the United States will be needed for steam-electric cooling water by 1980 (Krenkel and Parker 1969).

Fishes, like other organisms, are profoundly affected by temperature. Extensive bibliographies by Kennedy and Mihursky (1967) and Raney and Menzel (1969) attest to the wealth of available information regarding direct and indirect actions of temperature on the survival, growth, metabolism, behavior, and reproduction of fishes. Yet, ecological study of fishes in habitats heated by power plants began only about 15 years ago in North America, and such investigations are still few and incomplete. Coutant (1970, p. 376), in reviewing both published and unpublished information on "thermal pollution," concluded:

> Most power plant surveys lack detail of observation and definition of goals sufficient to provide more than circumstantial evidence for ecological processes . . . laboratory experiments are often unrealistic simulations of complex phenomena. True predictability will require judicious application of data from both sources.

Our investigation sought to avoid the deficiencies mentioned by Coutant (1970) and, in so doing, contribute to knowledge of the ecological processes that occur in aquatic habitats receiving heated effluent.

The Standpoint

Behavioral regulation of environment has been an under-emphasized feature in the ecology of fishes. Fishes are mobile organisms, able to swim through their habitat at sustained speeds of a few body lengths per second (Bainbridge 1960). In aquatic organisms with lesser potential for voluntary movements, physiological adaptation is perhaps the primary strategy for coping with environmental variation. Physiological mechanisms allow fishes also to successfully occupy diverse habitats and tolerate temporal fluctuations of environment.

But, if the potentially available environment is heterogeneous, a fish can behaviorally regulate the conditions it must experience by spending more time in one subset of environment and less or no time in other subsets.

Temperature heterogeneity of some aquatic habitats is greatly increased by their reception of heated effluents from steam-electric plants. Although the fraction of habitat near the point of effluent discharge (outfall area) may be warmed by several degrees Celsius, temperatures throughout most of the receiving water mass typically are unaltered. For example, only about 0.3% of the water at a depth of 0.5 m in Lake Monona is warmed more than 1 C by effluent from a power plant; the percentage of total volume so warmed is much smaller.

In a habitat partly heated by thermal effluent, then, temperatures experienced by fishes depend on where they live within the habitat. If fishes were randomly moving particles, the number exposed to elevated temperatures and the time each individual is exposed would be small. Fishes typically are not randomly distributed within a habitat; rather, they tend to be concentrated in some areas and scarce or absent in others.

Thus, the effects of steam-electric power production on fishes must depend first on their behavioral responses to elevated temperatures and to other features of the outfall area. It matters little whether in the laboratory yellow perch (*Perca flavescens*), for example, can grow at 30 C or can survive 33 C for 1,000 min if yellow perch never occur in an outfall area where temperatures exceed 29 C. The more important question is whether yellow perch given a choice will invade water of a particular temperature and, if so, for how long and for what reasons, ecologically prudent or otherwise. Only when fish are likely to occur voluntarily or by necessity under certain conditions does it become ecologically important to know the consequences of that exposure—consequences relative to survival, growth, and reproduction.

Major Objectives

Conviction that the responses of fishes to environmental variation are first manifest in their distributions prescribed the primary goals of the investigation. Major objectives were to:

1. assess spatial and temporal aspects of fish distribution in the outfall area of a steam-electric power plant;
2. relate fish distributions to temperature by measuring the temperatures at which fishes live during summer in the outfall area;
3. evaluate the relationship between fish

distributions during summer and behavioral thermoregulation; and

4. explore the extent to which fish may alter thermoregulatory behavior in order to acquire an essential resource—food.

Statistical Treatment of Data

To analyze data from both field and laboratory, nonparametric techniques were used almost exclusively. Reasons for avoiding more traditional, parametric methods included:

1. uncertainty about the level of measurements (in most cases, the data probably were of ordinal strength),
2. uncertainty about the shapes of the sampling distributions, and
3. small sizes of samples.

Confidence intervals for medians were constructed in accordance with the method suggested by Mood and Graybill (1963, p. 406). All other nonparametric tests used in this work were described by Siegel (1956). Infrequent recourse to parametric statistics is indicated by the word "parametric" and follows the usage of Steel and Torrie (1960).

FIELD RESEARCH SITE: LAKE MONONA

Lake Monona, in Wisconsin's Dane County, provides water for cooling the condensers of a coal and gas fired, 220-megawatt power plant operated by the Madison Gas and Electric Company. Water is removed from the lake (1,400 ha, maximum depth 22.5 m) at two points, each 5 m below the surface and about 110 m offshore. After a 10 C rise in temperature during circulation through the condensers, water is returned to the lake at two surface outfalls located about 200 m apart on the shoreline. Heated effluent flows almost continuously from the primary outfall but does not flow from the secondary outfall during periods of low power production. A steel-slatted baffle at the secondary outfall diffuses the jet; the primary jet is unobstructed. Operating capacities of the circulation pumps total 6,850 liters/sec (Hoopes, Zeller, and Rohlich 1968).

The heated discharge produces an area considerably warmer than the shallow water along the remainder of the shoreline. The fraction of the littoral zone less than 2 m deep and heated more than 1 C is about 2 ha.

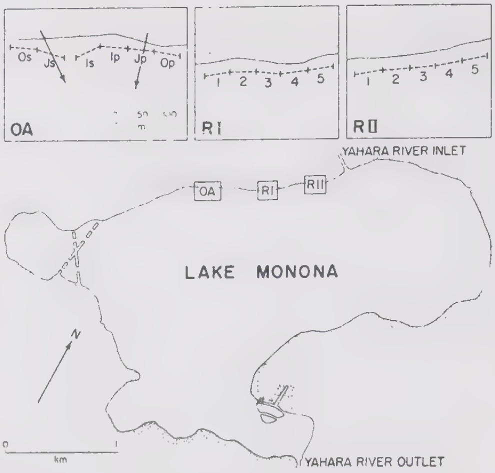

FIGURE 1.—Map of Lake Monona showing enlarged views of the outfall area (OA) and reference areas (RI and RII) with code letters for individual 50 m sampling transects (Os, Js, . . . , RII 5). Arrows indicate positions of the secondary jet (across transect Js) and primary jet (across transect Jp).

During winter, a plywood baffle supported by floating booms extends 2.5 m beneath the surface to surround 4.5 ha of the lake, including the outfall area. In midwinter, the baffled area is mostly free of ice except during the coldest weather. The baffle was installed in 1968 during the last week of November and removed the last week of February 1969.

Research effort was concentrated in the littoral zone near the effluent outfalls, termed outfall area or OA, and in two reference areas (Fig. 1). Reference areas I and II (RI and RII) were located about 600 and 1,300 m northeast of the outfall area and were more similar to the outfall area in bottom slope and type, aquatic vegetation, and exposure to winds than other locations. However, reference areas had more sand and less coarse gravel and rubble than the outfall area. The bottom in the outfall area was also more irregular and had a steeper slope. A channel about 2.5 m deep extended out from the primary outfall. The secondary jet passed over a sandy bar, 0.6 m deep, approximately 40 m offshore. The dominant macrophyte in outfall and reference areas was watermilfoil (*Myrio-*

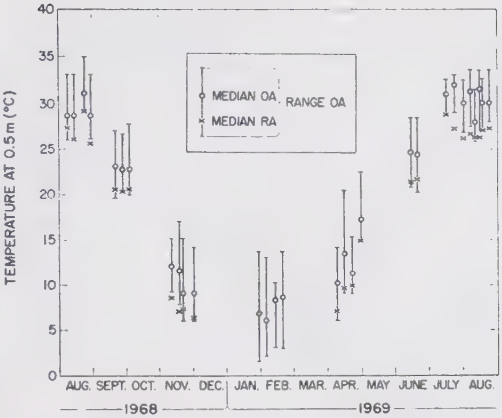

FIGURE 2.—Median temperatures of the outfall area and reference areas and range of temperature in the outfall area during each afternoon of fish sampling, 8 August 1968 to 21 August 1969.

phyllum), which sometimes was covered with growths of the filamentous alga *Cladophora*. However, the reference areas had more wild celery (*Vallisneria*) and common elodea (*Elodea*) than the outfall area.

Sixteen sampling transects were established, five in each reference area and six in the outfall area (Fig. 1). Each transect, 50 m long, was parallel to shore and along the 1–1.5 m bottom-contour interval. Transects Js and Jp spanned the secondary and primary jets, respectively; the other transects in the outfall area were positioned inside (Is and Ip) and outside (Os and Op) the area bounded by the jets. Transects were marked at each end by numbered buoys or by structures on shore.

WATER TEMPERATURE IN THE STUDY AREAS OF LAKE MONONA

Water temperatures were systematically measured during each phase of the investigation of fish distribution. As fishes were sampled, temperatures 0.5 m below the surface were continuously recorded with a Rustrak Thermistor Probe Recorder[2] (model 133). Temperatures at other depths were measured with an electronic thermometer of the Wheatstone-bridge type.

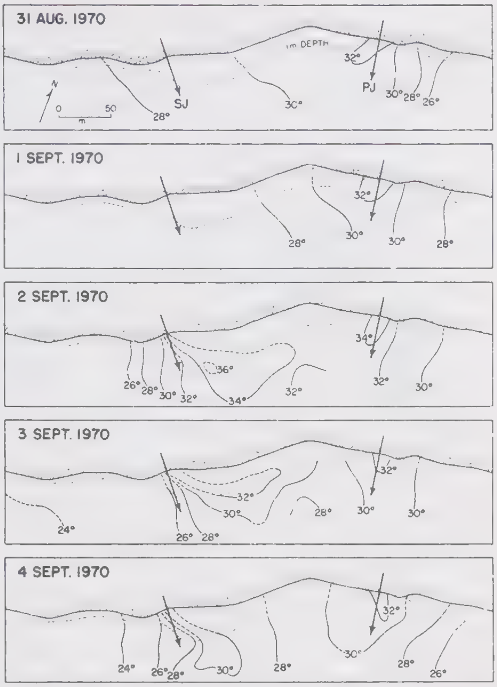

FIGURE 3.—Distribution of temperature at 0.5 m beneath the surface in the outfall area on five successive afternoons, 31 August–4 September 1970.

Water temperatures (0.5 m) in the reference areas were 25–30 C in August 1968 and, following the winter minimum, returned to similar levels in July and August 1969 (Fig. 2). The two reference areas had essentially identical temperatures. Minimum recorded temperature in the outfall area was similar to reference area temperatures on each sampling date. However, median and maximum temperatures in the outfall area exceeded reference area temperature by 2–4 C and 6–8 C, respectively, on most sampling dates. Temperatures at night were generally less than 2 C below those recorded during afternoon on the same date.

Median temperatures of transects on the same afternoon or evening varied less than 1 C within the reference areas but as much as 8.5 C in the outfall area. The transect across the primary jet (Jp) was 4–8 C warmer than the reference areas. Temperatures between the two jets (Ip and Is) were often fairly uniform and 3–5 C higher than those

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[2] Reference to trade names does not imply endorsement by The University of Wisconsin or by the National Marine Fisheries Service, NOAA.

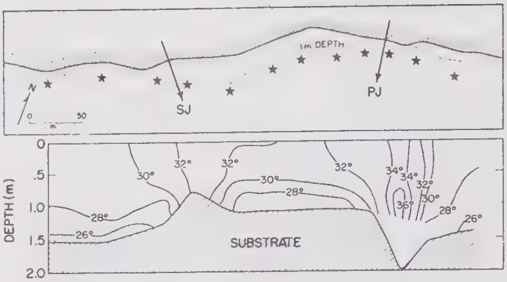

FIGURE 4.—Vertical distribution of temperature in the outfall area (afternoon, 17 August 1970). Stars on the plane view mark the locations where temperatures were measured.

of reference areas. The transect across the secondary jet (Js) was often cooler than that spanning the primary jet, even when heated effluent was flowing from the secondary outfall. Outside the jets, water temperature abruptly approached that of the reference areas.

Although some locations in the outfall area were consistently warmer than others, distribution of temperature varied greatly from day to day (Fig. 3) because of changes in wind velocity and variation in rates of effluent discharge. For example, on two consecutive afternoons about 18% and 66% of water at 0.5 m depth in the outfall area was warmer than 30 C (Fig. 3, 1 and 2 September 1970).

The outfall area was vertically stratified with respect to temperature (e.g., Fig. 4). Although water 0.5 m beneath the surface was usually less than 1 C cooler than surface water, water temperature at 1 m was often 3 C lower than at 0.5 m. (Surface and 1-m temperatures in the reference areas seldom differed by even 1 C.) Vertical stratification, always poorly defined near the jets, deteriorated throughout the outfall area when strong onshore winds promoted mixing.

DISTRIBUTION OF FISHES AMONG THE STUDY AREAS OF LAKE MONONA

Objectives

Electrofishing surveys were conducted in each study area to determine whether the different fishes of the littoral zone were relatively concentrated or scarce in the outfall area and whether the degree of concentration varied from day to night and from season to season.

Sampling Gear, Procedures, and Schedule

Fishes were captured with an electrofishing apparatus mounted on a pontoon barge (Fig. 5). Electricity (220 V-AC, 60 Hz) was supplied by a gasoline powered generator to three electrodes made from copper tubing 2.5 cm in diameter. The electrodes were suspended from booms projecting from the front of the barge; each electrode was weighted so that it hung vertically 1.4 m into the water. Immediately behind the electrodes, a push net with a 1- × 1.3-m rectangular opening collected stunned fishes from the top meter of water; the 2.5-m-long net of 6-mm mesh netting was lined in the final 1 m (purse) with 3-mm mesh netting (Fig. 5).

The sampling unit was one electrofishing run along a transect. During each 30- to 60-sec run, water temperature 0.5 m beneath the surface was continuously recorded, and water depth was measured several times.

Generally, all captured fishes were either preserved in 10% formalin or immediately identified, measured for total length, and released. However, catches of young bluegill (*Lepomis macrochirus*) were so large during summer and early fall 1968 that to preserve all of them was impractical. Bluegill less than 75 mm long from most night samples between 8 August and 30 November 1968 were disregarded. Except from 29 January to 19 June 1969, bluegill less than 75 mm long that were not actually in the purse of the net were disregarded. Larger bluegill and all other fishes were recorded, regardless of their final position within the net.

Most larger fishes to be released were marked in 1968 by a fin-punch distinctive for the area of capture, or in 1969 by a

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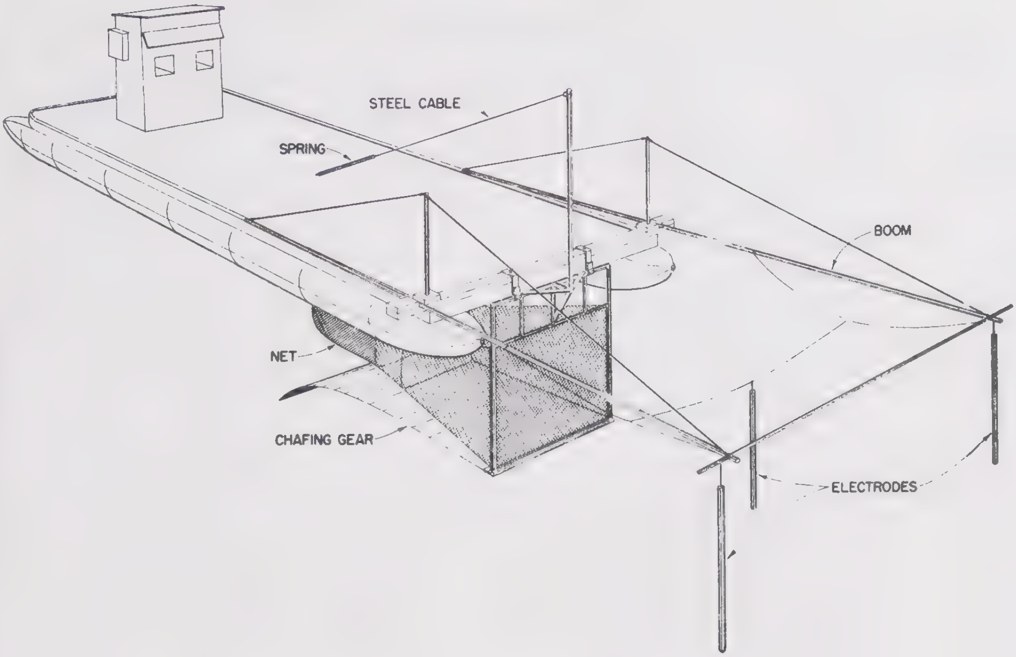
FIGURE 5.—Diagram of the barge rigged for electrofishing and a detailed view of the push net.


STEEL CABLE
SPRING
BOOM
NET
CHAFING GEAR
ELECTRODES

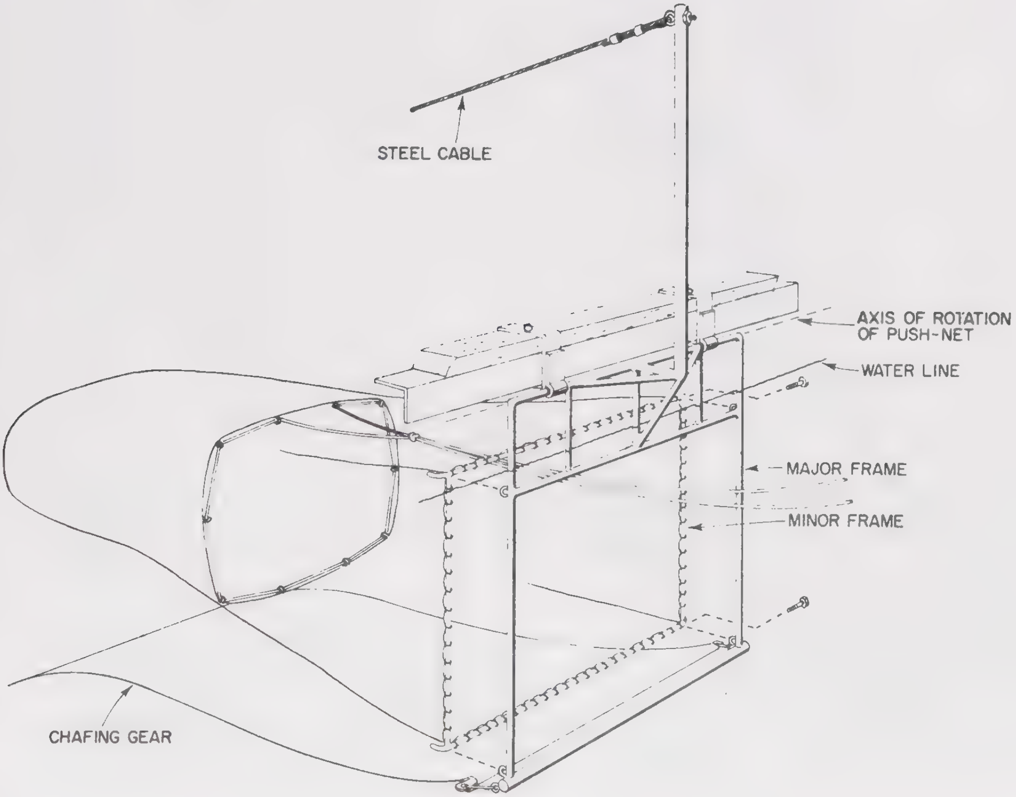

STEEL CABLE
AXIS OF ROTATION OF PUSH-NET
WATER LINE
MAJOR FRAME
MINOR FRAME
CHAFING GEAR

TABLE 1.—*Species, lengths, and numbers of fish caught from the study areas of Lake Monona during electrofishing surveys, 8 August 1968 to 21 August 1969*

Species		Length class identification	Range of total lengths (mm)	Total number caught
Common name	Scientific name			
Longnose gar	*Lepisosteus osseus* (Linnaeus)	—	365–846	43[a]
Northern pike	*Esox lucius* Linnaeus	—	229–531	2
Carp	*Cyprinus carpio* Linnaeus	small	8–123	160
Carp	*Cyprinus carpio* Linnaeus	large	163–737	96
Golden shiner	*Notemigonus crysoleucas* (Mitchill)	—	17–115	21
Emerald shiner	*Notropis atherinoides* Rafinesque	—	80	1
Spottail shiner	*Notropis hudsonius* (Clinton)	—	98–100	3
Bluntnose minnow	*Pimephales notatus* (Rafinesque)	—	17–68	20
White sucker	*Catostomus commersoni* (Lacépède)	—	403–460	4
Bigmouth buffalo	*Ictiobus cyprinellus* (Valenciennes)	—	440–600	7
Black bullhead	*Ictalurus melas* (Rafinesque)	small	33–150	165
Black bullhead	*Ictalurus melas* (Rafinesque)	large	151–265	46
Yellow bullhead	*Ictalurus natalis* (Lesueur)	—	226–245	2
Brown bullhead	*Ictalurus nebulosus* (Lesueur)	—	63–230	12
Banded killifish	*Fundulus diaphanus* (Lesueur)	—	38–64	2
Brook silverside	*Labidesthes sicculus* (Cope)	—	8–97	413
Brook stickleback	*Culaea inconstans* (Kirtland)	—	29	1
White bass	*Morone chrysops* (Rafinesque)	—	17–294	33
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	small	13–50	417
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	medium	51–99	187
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	large	107–256	287
Rock bass	*Ambloplites rupestris* (Rafinesque)	small	10–48	120
Rock bass	*Ambloplites rupestris* (Rafinesque)	large	51–210	54
Green sunfish	*Lepomis cyanellus* Rafinesque	—	19–166	17
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)	small	12–75	149
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)	large	76–170	136
Bluegill	*Lepomis macrochirus* Rafinesque	small	28–75	19,154
Bluegill	*Lepomis macrochirus* Rafinesque	medium	76–100	237
Bluegill	*Lepomis macrochirus* Rafinesque	large	101–224	848
Largemouth bass	*Micropterus salmoides* (Lacépède)	—	51–311	77
White crappie	*Pomoxis annularis* Rafinesque	—	114–247	10
Black crappie	*Pomoxis nigromaculatus* (Lesueur)	small	12–75	853
Black crappie	*Pomoxis nigromaculatus* (Lesueur)	large	76–249	81
Iowa darter	*Etheostoma exile* (Girard)	—	23–89	65
Johnny darter	*Etheostoma nigrum* Rafinesque	—	65	1
Yellow perch	*Perca flavescens* (Mitchill)	small	46–99	285
Yellow perch	*Perca flavescens* (Mitchill)	large	101–286	99
Logperch	*Percina caprodes* (Rafinesque)	—	35–117	44
Walleye	*Stizostedion vitreum vitreum* (Mitchill)	—	13–585	41
Freshwater drum	*Aplodinotus grunniens* Rafinesque	—	68–420	53
Mottled sculpin	*Cottus bairdi* Girard	—	31–83	93

[a] Includes sighted as well as captured longnose gar.

numbered anchor tag (Floy Anchor Tag, FD-67) inserted into the epaxial musculature beneath the dorsal fin.

Fish distributions were surveyed on 30 dates from 8 August 1968 to 21 August 1969. Generally, each transect was sampled twice on every date, once during the afternoon [1230–1730 CST (central standard time)] and again after dark (1830–2400 CST). However, the reference areas were not sampled during January and February 1969 because ice covered them.

Analytical Treatment of Fish-Catch Data

Analyses of distributions were based on catch per unit effort (catch/effort). Catch data were categorized by species, length class, season, time of day, and location of capture. Individuals of each species were pooled into one, two, or three length classes, the number

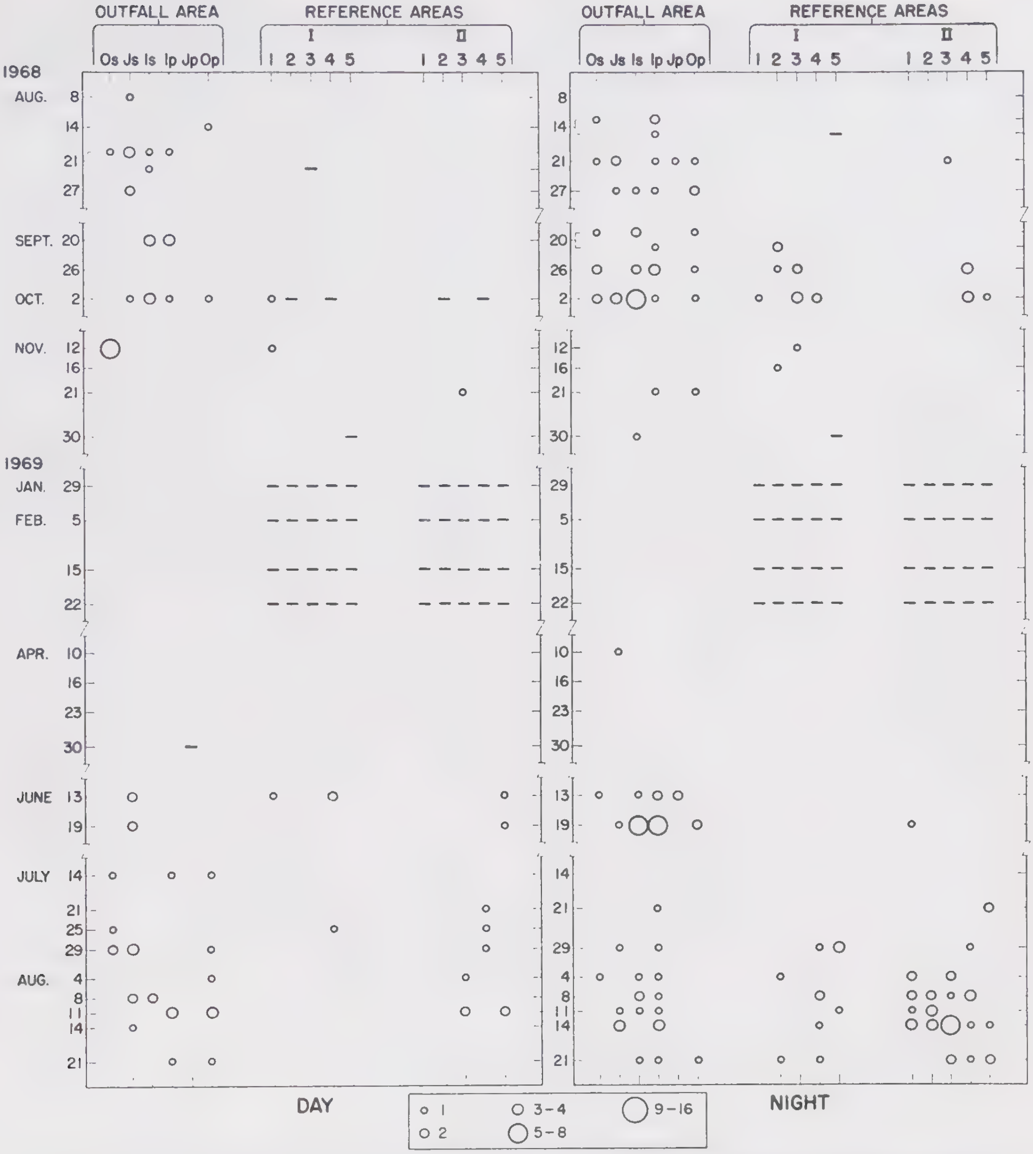


FIGURE 6.—Number of medium bluegill caught from each electrofishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.

of classes increasing with the number of specimens (Table 1). Two length classes approximately separated yearling and younger fish from those older than 1 year; three length classes approximately separated age 0, age I, and older fish. Sampling dates clustered temporally and thermally into seven seasonal periods: (1) August 1968, (2) September–October 1968, (3) November 1968, (4) January–February 1969, (5) April 1969, (6) June 1969, and (7) July–August 1969 (Fig. 2). The minimum and maximum time inter-

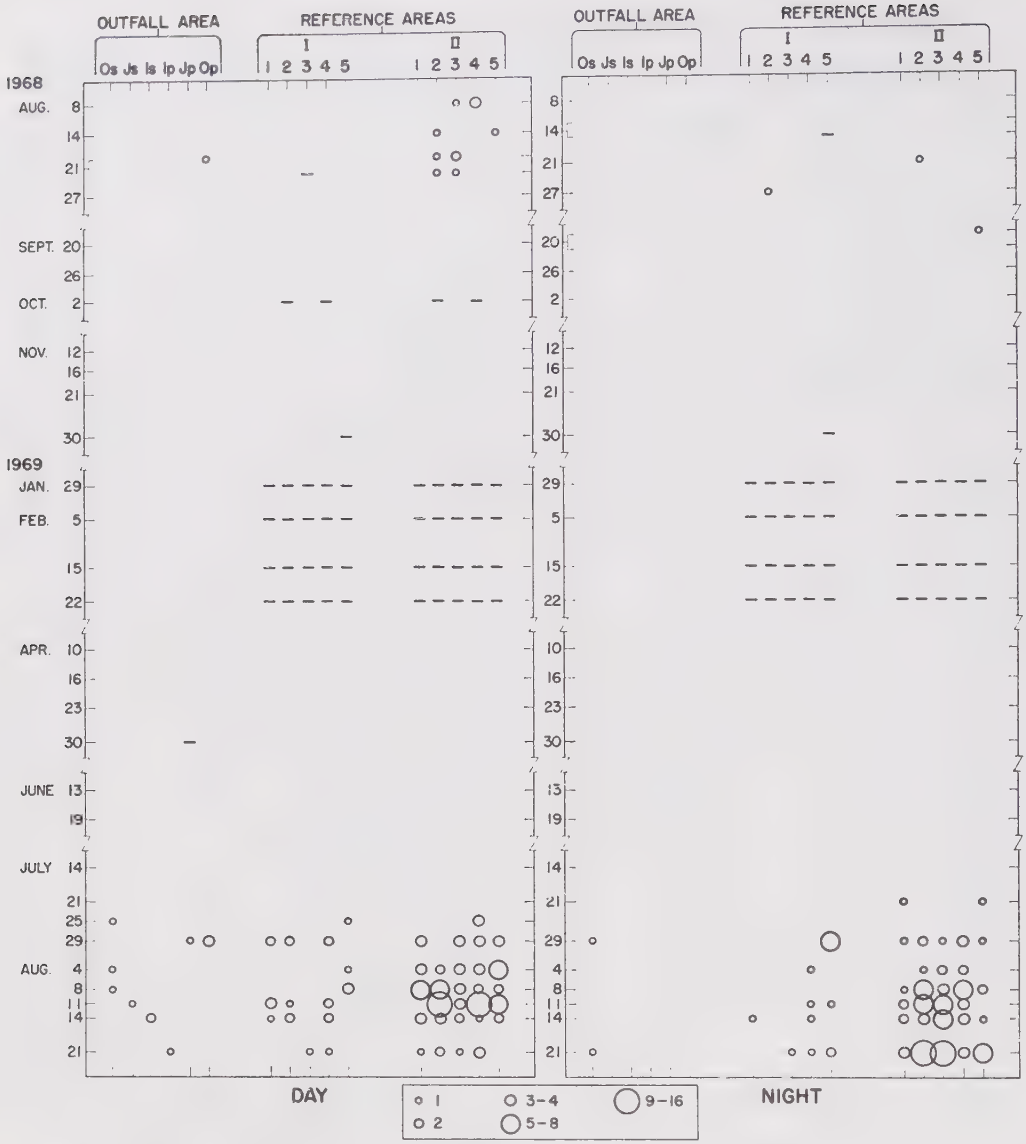


FIGURE 7.—Number of small yellow perch caught from each electrofishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.

vals between successive sampling dates of any period were 3 and 9 days. Reference area temperatures were between 25 and 30 C during August 1968 and July–August 1969, between 20 and 22 C during September–October 1968 and June 1969, between 6 and 15 C during November 1968 and April 1969, and between 0 and 4 C during January–February 1969 (Fig. 2). Within each season, day and night catches were considered separately.

For each category of catch, catch/effort from the outfall area was compared statistically with that from the combined reference areas. The null hypothesis that catch/effort from the outfall area equaled catch/effort from the reference areas was assessed by the Kolmogorov-Smirnov one-sample test, a distribution-free analysis for goodness of fit. Statements concerning different abundances of fishes between areas are inferences based on significant ($p \leqslant 0.05$) differences in catch/effort.

Catches of most fishes varied greatly with season and time of day (e.g., Figs. 6 and 7). Young fishes were represented mostly in summer and fall samples; larger individuals of many species were caught more frequently at night than during afternoon. Thus, for any one species and length class, comparison of catch/effort between outfall and reference areas was limited to only certain of the seasonal-diel periods. Comparisons between areas were automatically precluded for the January–February 1969 period because the reference areas were not sampled.

Abundance of Fishes in the Outfall Area Relative to Reference Areas

Of the 31 species collected, 11 were unevenly distributed between outfall and reference areas during at least one seasonal-diel period (Fig. 8).

Longnose gar (*Lepisosteus osseus*) were conspicuously concentrated in the outfall area at night during both summers. A small fraction of individuals, once stunned, actually entered the push net; most longnose gar swam erratically and violently out of the electrical field, escaping capture. Beginning in 1969, we systematically tallied longnose gar only seen by the push net operator as well as those actually caught. These data indicated that longnose gar were more abundant in the outfall area than in the reference areas at night in July–August 1969. The same was undoubtedly true in August 1968, although few quantitative data were collected. Few longnose gar were seen or caught during other sampling periods. All captured longnose gar and probably all those only sighted exceeded 350 mm in length.

Large carp (*Cyprinus carpio*) were more abundant in the outfall area than in the reference areas during August 1968, day and night; September–October 1968, day and night; November 1968, night; and July–August 1969, night. In contrast, during both day and night in August 1968 and again in July–August 1969, small fish (most <25 mm long) tended to be less abundant in the outfall area than in the reference areas, the ratio of catch/effort from the outfall area to catch/effort from the reference areas never exceeding 0.67. But during any one seasonal-diel period, catch/effort of small carp from the outfall area did not differ significantly from that in the combined reference areas.

Small black bullhead (*Ictalurus melas*) were more abundant in the reference areas than in the outfall area during November 1968, day and night. During both summers, large schools of age 0 black bullhead were frequently seen in the reference areas but rarely in the outfall area.

Large yellow bass (*Morone mississippiensis*) were more abundant by day in the outfall area than in the reference areas during April 1969, June 1969, and July–August 1969. But at night their abundances in outfall and reference areas did not differ significantly during August 1968, September–October 1968, April 1969, or July–August 1969, even though sample size was relatively large, exceeding 40 fish during each season. Catch/effort was higher at night than during the day. Small and medium-sized yellow bass were more abundant, day and night, in reference areas than in the outfall area during July–August 1969.

Large yellow bass in the outfall area were concentrated near the discharge jets, particularly during the day. Although runs across the two jets constituted only 33% of sampling effort in the outfall area, they produced 96% (25 of 26 fish) and 66% (63 of 95 fish) of the large yellow bass caught in the outfall area during day and night, respectively. During late winter and spring 1969, adult yellow bass (in addition to bluegill and black crappie) were conspicuously concentrated at the primary outfall during the daylight hours; these fish were not effectively sampled by electrofishing.

Small rock bass (*Ambloplites rupestris*) were more abundant in the outfall area than in the reference areas during July–August

1969, day and night. Of 77 specimens caught from the outfall area during July–August 1969, the two coolest transects, Op and Os, yielded 33 and 30 fish, respectively. The remaining 14 fish were all caught from Js, the southwest end of which was generally cooler than water between or in the jets.

Although 29 and 73 large pumpkinseed (*Lepomis gibbosus*) were caught during day and night sampling in July–August 1969, outfall and reference area catch/effort did not differ significantly. Small pumpkinseed were more abundant in the outfall area than in reference areas during both day and night in August 1968 and during afternoon in September–October 1968.

Bluegill were caught much more frequently than any other species; 848 large, 237 medium, and over 19,000 small specimens were taken.

Large and medium-sized bluegill were more abundant by day in the outfall area than in the reference areas during August 1968, September–October 1968, November 1968, and July–August 1969. Large bluegill were more abundant at night in the outfall area than in the reference areas during all seasonal periods except August 1968 and July–August 1969; at night, medium-sized bluegill were more abundant in the outfall area than in the reference areas during August 1968, September–October 1968, and June 1969.

Small bluegill were more abundant, both day and night, in the outfall area than in the reference areas during August 1968 and July–August 1969, and, at least by day, in September–October 1968 and June 1969, as well. In November 1968, however, young bluegill during the day were more abundant in reference areas than in the outfall area.

During both years age 0 bluegill were taken in progressively increasing numbers as summer advanced, but mid-August catches in 1969 were only about 20% of those in 1968. Catch/effort in 1968 declined during November from the maximum reached in September. Reference area I produced a much smaller fraction of the total young bluegill catch in July–August 1969 than in August 1968.

Largemouth bass (*Micropterus salmoides*) were more abundant by day in the outfall area than in the reference areas during September–October 1968 and July–August 1969. Largemouth bass were more evenly distributed among areas at night.

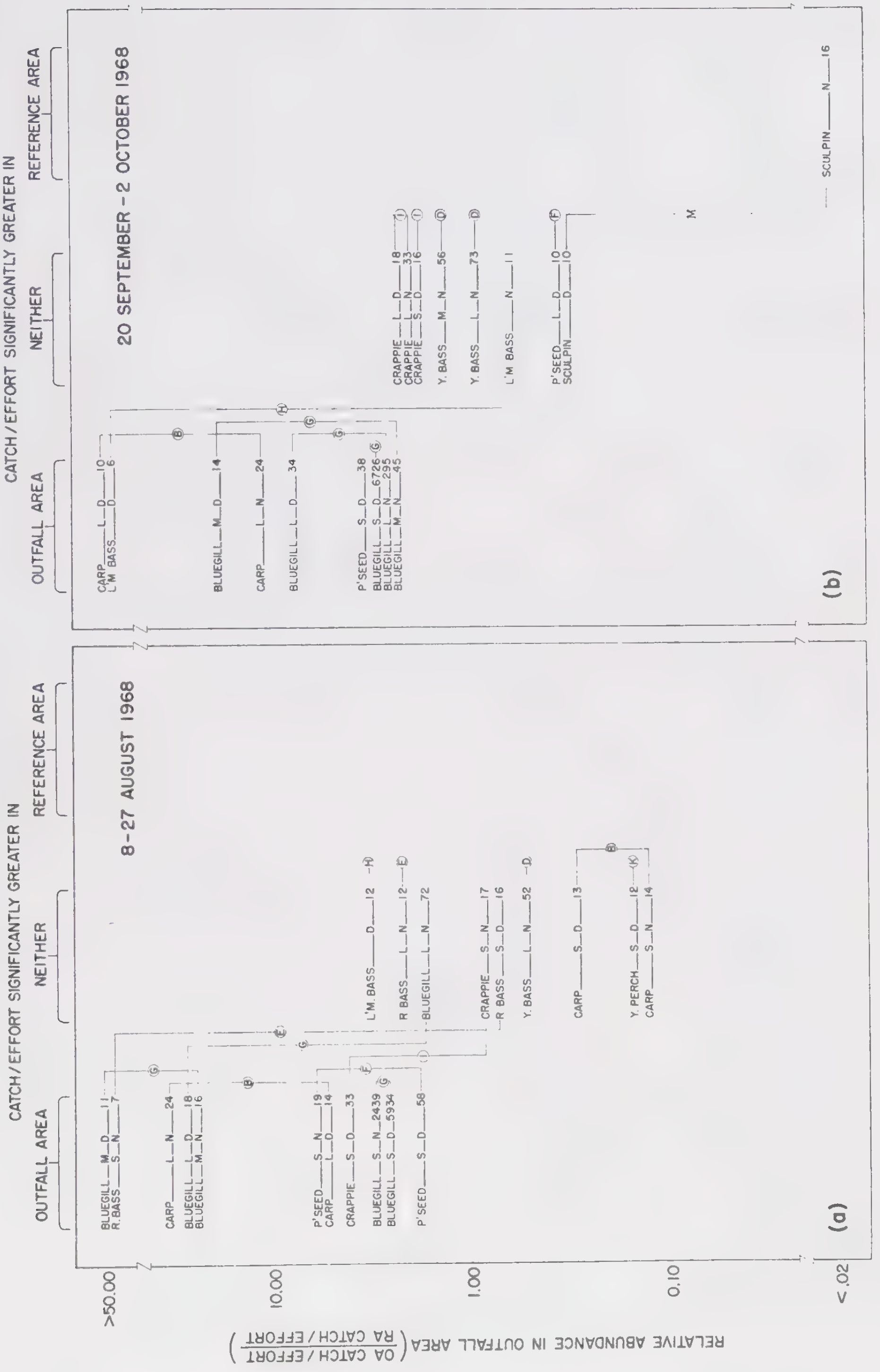
Small black crappie (*Pomoxis nigromaculatus*) were more abundant by day in the outfall area than in reference areas in August 1968, but they were more abundant in the reference areas during both day and night in July–August 1969. Large fish tended to be more abundant in the outfall area than in the reference areas during September–October 1968, but neither day nor night catches differed significantly between areas.

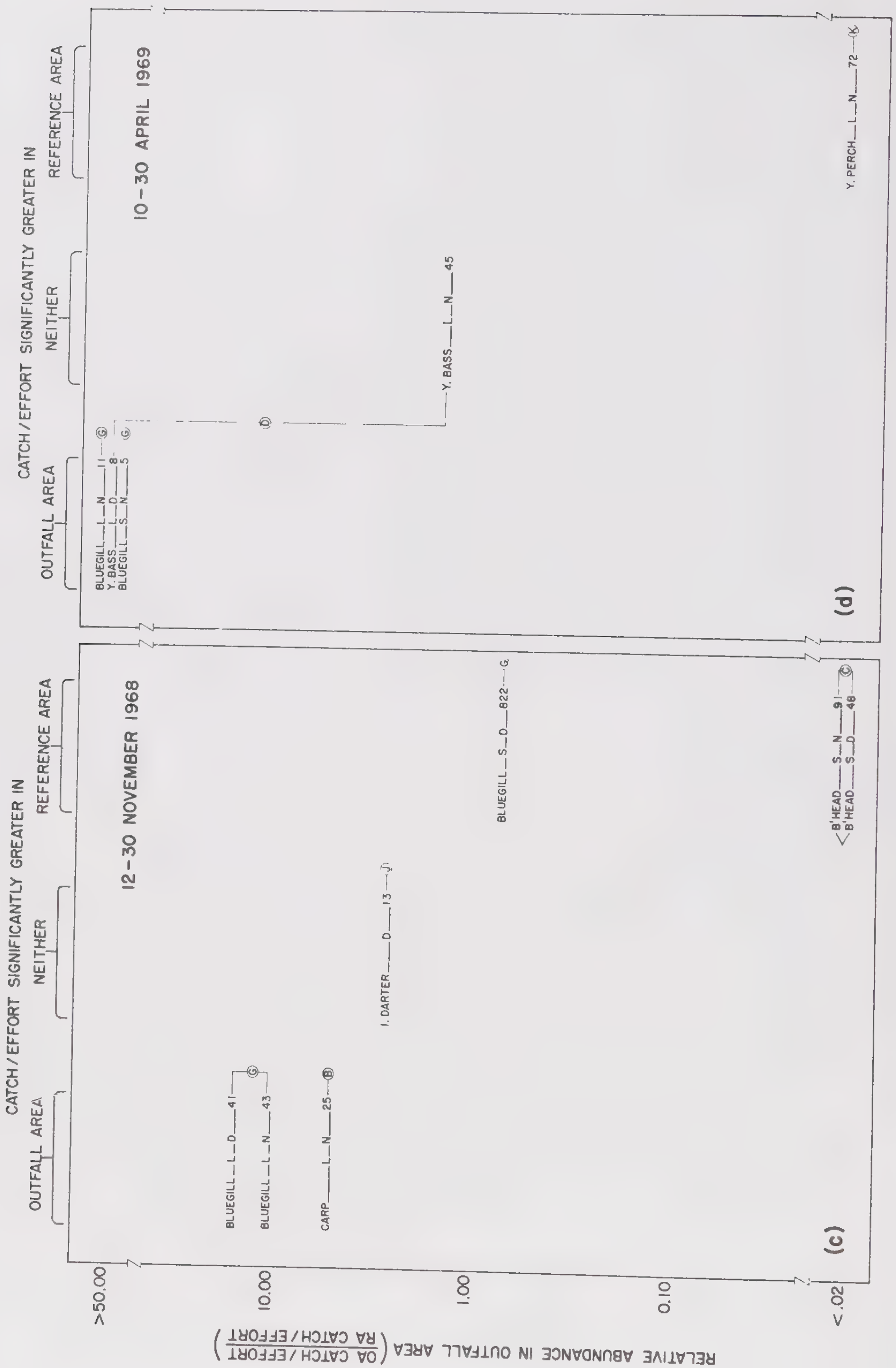
Few large yellow perch were taken, except at night during April 1969. All of these were caught from the reference areas; RII produced more fish than RI. All specimens examined were ripe males. Yellow perch egg masses

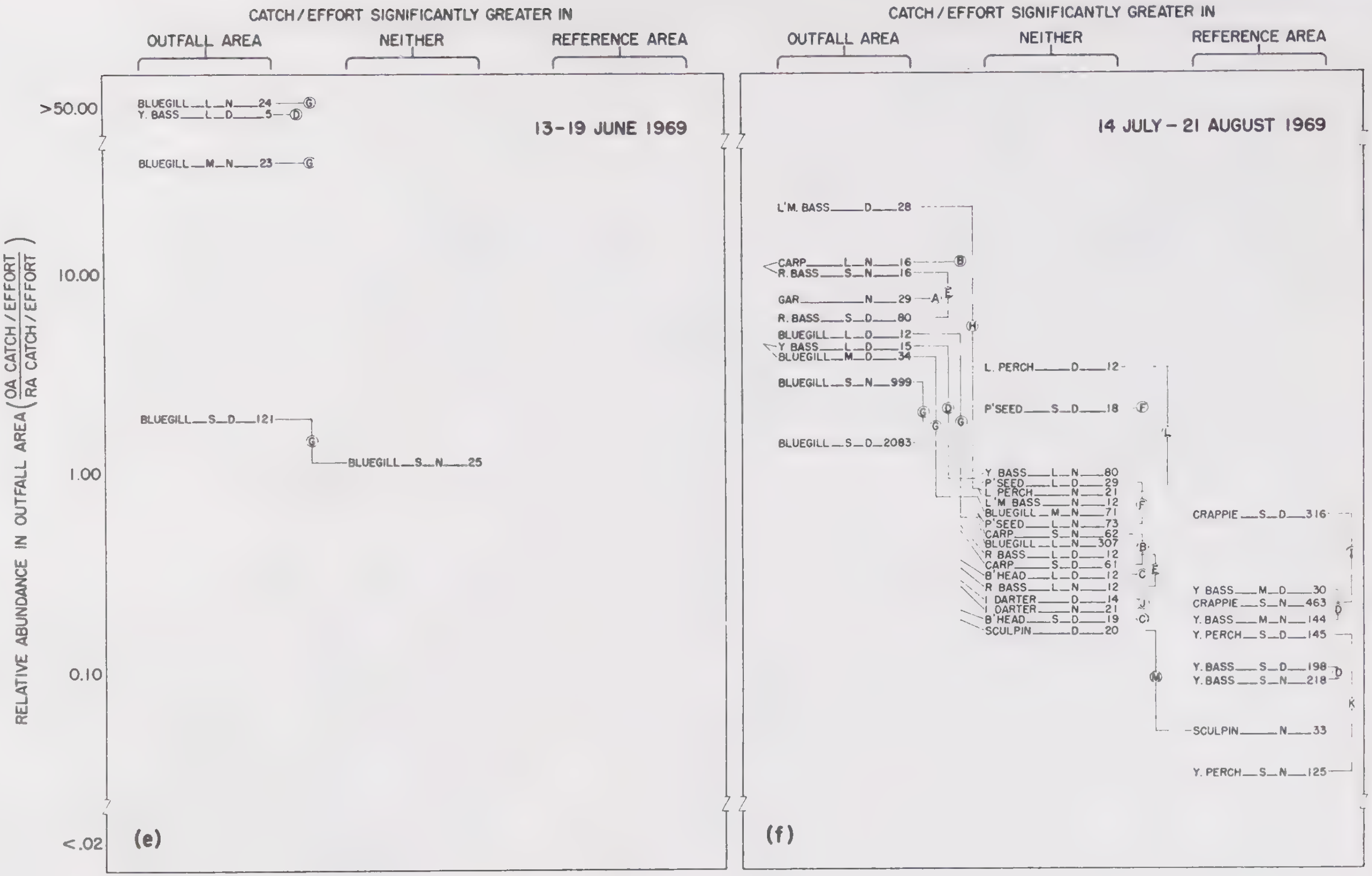
→

FIGURE 8.—Comparison of electrofishing catch/effort between outfall and combined reference areas by season: (a) August 1968, (b) September–October 1968, (c) November 1968, (d) April 1969, (e) June 1969, (f) July–August 1969. The vertical position of each entry is a measure of the degree to which fish were concentrated in the outfall area relative to reference areas; the horizontal position of each entry indicates whether catch/effort from the outfall area was statistically greater than, not different from, or less than catch/effort from the reference areas (Kolmogorov-Smirnov one-sample test; probability level, 0.05). Each entry consists of fish of one species and length class (L = large, M = medium, S = small, no letter = all lengths; see Table 1 for identification of length classes) caught during one time of day (D = afternoon, N = night); the number of fish follows the code letter for time of day. Lines from entries extend to encircled letters (see below) and connect day and night entries for fish of the same species-length category if both day and night data were obtained.

A	Longnose gar	H	Largemouth bass
B	Carp	I	Black crappie
C	Black bullhead	J	Iowa darter
D	Yellow bass	K	Yellow perch
E	Rock bass	L	Logperch
F	Pumpkinseed	M	Mottled sculpin
G	Bluegill		


CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
8-27 AUGUST 1968
20 SEPTEMBER - 2 OCTOBER 1968
(a)
(b)
RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH / EFFORT / RA CATCH / EFFORT)
>50.00
10.00
1.00
0.10
<.02
BLUEGILL M D 11
R. BASS S N 7
CARP L N 24
BLUEGILL L D 18
BLUEGILL M N 16
P'SEED S N 19
CARP L D 14
CRAPPIE S D 33
BLUEGILL S N 2439
BLUEGILL S D 5934
P'SEED S D 58
L'M. BASS D 12
R BASS L N 12
BLUEGILL L N 72
CRAPPIE S N 17
R BASS S D 16
Y. BASS L N 52
CARP S D 13
Y. PERCH S D 12
CARP S N 14
CARP L D 10
L'M BASS D 6
BLUEGILL M D 14
CARP L N 24
BLUEGILL L D 34
P'SEED S D 38
BLUEGILL S D 6726
BLUEGILL L N 295
BLUEGILL M N 45
CRAPPIE L D 18
CRAPPIE L N 33
CRAPPIE S D 16
Y. BASS M N 56
Y. BASS L N 73
L'M BASS N 11
P'SEED L D 10
SCULPIN D 10
SCULPIN N 16
M
B
D
E
F
G
H
I
K


RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH/EFFORT / RA CATCH/EFFORT)
>50.00
10.00
1.00
0.10
< .02
CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
12-30 NOVEMBER 1968
BLUEGILL—L—D—41—G
BLUEGILL—L—N—43—G
CARP—L—N—25—B
I. DARTER—D—13—J
BLUEGILL—S—D—822—G
<B'HEAD—S—N—91—C
<B'HEAD—S—D—48—C
(c)
CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
10-30 APRIL 1969
BLUEGILL—L—N—11—G
Y. BASS—L—D—8—G
BLUEGILL—S—N—5—G
D
Y. BASS—L—N—45
Y. PERCH—L—N—72—K
(d)


CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH/EFFORT / RA CATCH/EFFORT)
>50.00
10.00
1.00
0.10
<.02
13-19 JUNE 1969
BLUEGILL L N 24 G
Y. BASS L D 5 D
BLUEGILL M N 23 G
BLUEGILL S D 121
G
BLUEGILL S N 25
(e)
14 JULY - 21 AUGUST 1969
L'M. BASS D 28
CARP L N 16 B
R. BASS S N 16
GAR N 29 A E
R. BASS S D 80
H
BLUEGILL L D 12
Y BASS L D 15
BLUEGILL M D 34
BLUEGILL S N 999
G G D G
BLUEGILL S D 2083
L. PERCH D 12
P'SEED S D 18 F
L
Y BASS L N 80
P'SEED L D 29
L PERCH N 21
L'M BASS N 12
BLUEGILL M N 71
P'SEED L N 73
CARP S N 62
BLUEGILL L N 307
R BASS L D 12
CARP S D 61
B'HEAD L D 12
R BASS L N 12
I DARTER D 14
I DARTER N 21
B'HEAD S D 19
SCULPIN D 20
F
B
C E
J
C
M
CRAPPIE S D 316
I
Y BASS M D 30
CRAPPIE S N 463
Y. BASS M N 144
Y. PERCH S D 145
D
Y. BASS S D 198
Y. BASS S N 218
D
K
SCULPIN N 33
Y. PERCH S N 125
(f)

were frequently observed during April in both reference areas. Small yellow perch were more abundant in the reference areas (primarily RII) than in the outfall area during both day and night in July–August 1969 (Fig. 7).

Mottled sculpin (*Cottus bairdi*) were more abundant in the reference areas than in the outfall area at night during September–October 1968 and during both day and night in July–August 1969.

Although 20 other species (approximately 800 individuals) were caught, catch data did not strongly indicate nonuniformity in their spatial distributions. Brook silverside (*Labidesthes sicculus*) were probably concentrated in the outfall area during summer and early fall. Large schools of brook silverside were regularly observed near the primary jet, but these small fish were seldom stunned by the electrical field and usually escaped the push net. Seven bigmouth buffalo (*Ictiobus cyprinellus*) were caught during fall 1968; all were taken in runs across the primary jet. We saw other bigmouth buffalo swimming in the primary discharge plume but never elsewhere.

The extent to which littoral distributions of Lake Monona fishes were biased in favor of or against the outfall area may be summarized by segregating several response types. Segregation is achieved by a dichotomous key used in the same manner as those constructed for taxonomic identifications:

1a Catch/effort not significantly different between outfall and reference areas during any seasonal-diel period 2
1b Catch/effort significantly different between outfall and reference areas during at least one seasonal-diel period 3
2a Fewer than 20 specimens caught during any seasonal-diel period .... Rare types
    Northern pike (*Esox lucius*)
    Golden shiner (*Notemigonus crysoleucas*)
    Emerald shiner (*Notropis atherinoides*)
    Spottail shiner (*Notropis hudsonius*)
    Bluntnose minnow (*Pimephales notatus*)
    White sucker (*Catostomus commersoni*)
    Bigmouth buffalo
    Black bullhead, large
    Yellow bullhead (*Ictalurus natalis*)
    Brown bullhead (*Ictalurus nebulosus*)
    Banded killifish (*Fundulus diaphanus*)
    White bass (*Morone chrysops*)
    Rock bass, large
    Brook stickleback (*Culaea inconstans*)
    Green sunfish (*Lepomis cyanellus*)
    White crappie (*Pomoxis annularis*)
    Johnny darter (*Etheostoma nigrum*)
    Walleye (*Stizostedion vitreum vitreum*)
    Freshwater drum (*Aplodinotus grunniens*)
2b At least 20 specimens caught during some seasonal-diel period .... Indifferent types
    Carp, small
    Pumpkinseed, large
    Black crappie, large
    Iowa darter (*Etheostoma exile*)
    Logperch (*Percina caprodes*)
3a Catch/effort in the reference areas never significantly less than in the outfall area .... Reference-area types
    Black bullhead, small
    Yellow bass, small & medium
    Yellow perch, small & large
    Mottled sculpin
3b Catch/effort in the outfall area significantly greater than in the reference areas during at least one seasonal-diel period 4
4a Catch/effort in the reference areas significantly greater than in the outfall area during at least one seasonal-diel period .... Mixed types
    Bluegill, small
    Black crappie, small
4b Catch/effort in the outfall area never significantly less than in the reference areas .... Outfall-area types
    Longnose gar
    Carp, large
    Yellow bass, large
    Rock bass, small
    Pumpkinseed, small
    Bluegill, medium & large
    Largemouth bass

The key perhaps misrepresents the responses of some fishes. Small carp were probably more abundant during summer in the reference areas. Small bluegill were more abundant in the reference areas in November 1968 but were more abundant in the outfall area during most other seasons. Large black crappie were probably more abundant in outfall than in reference areas during September–October 1968. Thus, small carp may have been a reference-area type, whereas both small bluegill and large black crappie were probably outfall-area types.

There were no reference data with which to compare catches in the outfall area during January–February 1969, but electrofishing and visual observation suggested that fishes present in the outfall area were few compared with numbers there at other seasons. Twenty-four day and 24 night runs yielded only 31 specimens representing six species: 13 bluegill, 10 brook silverside, 3 Iowa darter, 2 carp, 2 golden shiner, and 1 yellow bass. Aquatic vegetation was essentially absent from the entire outfall area during winter.

Recapture of Marked Fishes

Although 934 fishes were fin-punched during 1968 and 1,726 more were tagged in 1969, we had recaptured only eight marked specimens by 1 July 1970. Forty-two tagged specimens were caught and reported to us by fishermen. Of 14 yellow bass and 21 bluegill reported by fishermen, 10 and 12 fish, respectively, were caught more than 1 km from the tagging location. These data verified that we were not catching and re-catching the same individuals. They also supported our general impression that residence times of larger fishes in the sampling areas were short—1 week or less.

Distribution of Lake Monona Fish Compared with That of Fishes in Other Heated Waters

Little published literature exists on the distributions of fishes in other waters receiving heated effluent (Raney and Menzel 1969; Coutant 1970). No published field study and only a fraction of the report literature with which we are acquainted deal with a lake environment or an ichthyofauna very similar to that of Lake Monona. However, most information now available suggests that whatever the habitat type and ichthyofaunal composition, some species avoid effluent outfall areas while others concentrate there.

Alabaster and Downing (1966) observed that fish distributions were little altered by effluents that warmed only the surface layers of several British rivers; but, in the more thoroughly mixed River Trent, bream (*Abramis brama*), tench (*Tinca tinca*), and carp lived in the warmest water available (about 28 C), while roach (*Rutilus rutilus*) and gudgeon (*Gobio gobio*) avoided water warmer than 26 C. Trembley (1961) reported that satinfin shiner (*Notropis analostanus*), banded killifish, American eel (*Anguilla rostrata*), redbreast sunfish (*Lepomis auritus*), and bluegill occurred during summer at temperatures above 32 C in the effluent lagoon of a power plant on the Delaware River, Pennsylvania. During cooler weather, the lagoon was inhabited by additional species, including golden shiner, brown bullhead, largemouth bass, black crappie, pumpkinseed, and rock bass. During summer in the Wabash River (Indiana) carp, buffalo (*Ictiobus* sp.), longnose gar, and channel catfish (*Ictalurus punctatus*) were among species concentrated below a heated effluent outfall (>30 C), but river carpsucker (*Carpiodes carpio*), redhorse (*Moxostoma* sp.), spotted bass (*Micropterus punctulatus*), longear sunfish (*Lepomis megalotis*), and sauger (*Stizostedion canadense*) were more abundant upstream from the outfall (Gammon 1970). Carp, buffalo, and channel catfish, but also river carpsucker and longear sunfish, occurred in summer at temperatures exceeding 33 C in an effluent canal discharging into the White River, Indiana (Proffitt 1969). Threadfin shad (*Dorosoma petenense*), sauger, skipjack herring (*Alosa chrysochloris*), and channel catfish concentrated in a heated discharge harbor on Kentucky Lake, Tennessee, during winter and spring (Dryer and Benson 1957). In marine environments, too, some fishes apparently concentrate near heated discharge outfalls, while others seem less abundant than in unheated areas (Allen, Boydstun, and Garcia 1970).

Insofar as similarity of species compositions allowed comparison, responses of adult fishes in Lake Monona were similar to their responses at other sites. Longnose gar, carp, bigmouth buffalo, bluegill, largemouth bass, black crappie, pumpkinseed, and rock bass—all recorded from other heated waters—did not avoid the outfall area of Lake Monona, although actual concentrations of adult black crappie, pumpkinseed, and rock bass were not demonstrated in the outfall area. At other sites, distributional data have not been collected for those fishes that avoided the outfall area of Lake Monona.

We are aware of no quantitative information on the distributions of young fishes relative to heated discharges, except for those data we collected in Lake Monona, nor have nocturnal distributions of fishes at other sites been investigated. But perhaps size and diel differences like those observed in Lake Monona are typical of fish distributions in heated environments.

Three field studies (Dryer and Benson 1957; Trembley 1961; Proffitt 1969) suffered a common deficiency: suitable reference sites, with which the discharge area could be

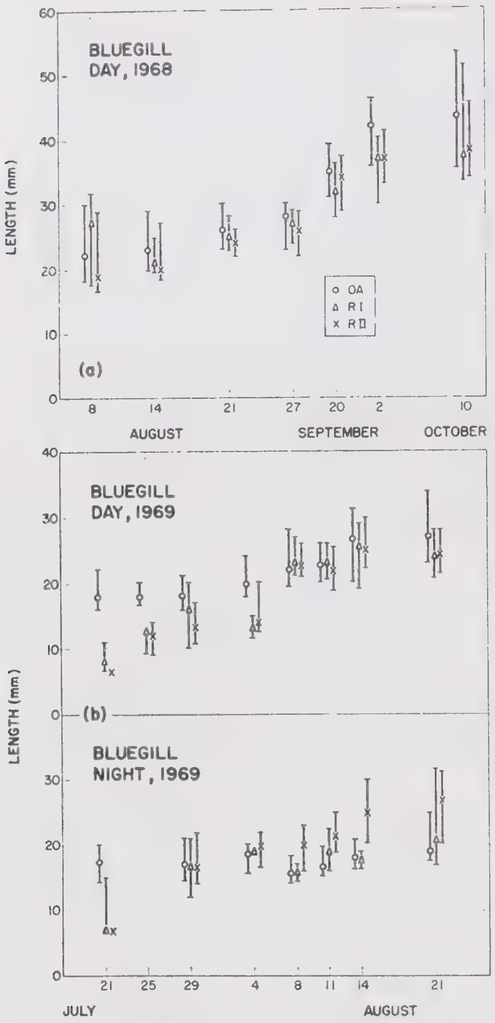


FIGURE 9.—Length-frequency distributions of age 0 bluegill collected from each study area, 8 August–10 October 1968 (a), and 21 July–21 August 1969 (b). Medians are indicated by point symbols; vertical lines are interquartile ranges. Sample size was at least 10 fish in each case during 1968 and at least five fish in most cases during 1969.

compared, were unavailable. Therefore, responses of fishes to the discharge area at one season could only be judged by those during some other season or reconciled with general impressions of fish distributions in the body of water as a whole. Thus, ". . . a remarkably common phenomenon, i.e., the attraction of fish to warmed water (from power plants) during cooler months and repulsion by thermal extrèmes in the peak of summer" (Coutant 1970, p. 367) must be interpreted with some caution.

Whatever occurs seasonally in heated discharge areas may also occur simultaneously in other similar, but unheated, parts of the habitat. For example, apparent abundances of several fishes fluctuated seasonally in the outfall area of Lake Monona, but similar fluctuations occurred simultaneously in the reference areas. Ratios of outfall to reference area catch/effort fluctuated to a lesser extent. Only among small bluegill and small black crappie were there significant reversals in the ratio from one season to another. In the black crappie, reversal occurred from one summer to the next, a change that could not be attributed to temperature. Young bluegill were more abundant in the outfall area during both summers but were more abundant in the reference areas during a colder season, November 1968. In Lake Monona, fishes did not differentially avoid the outfall area during summer to a much greater extent than at other seasons. Nor were the numbers of fish present in the outfall area during January–February 1969 as great as in summer.

Whatever difficulties arise in the assessment of fish abundances in outfall areas in the absence of suitable control sites, there can be little doubt that some spectacular concentrations of fishes do occur in direct response to the operation of power plants. For example, Dryer and Benson (1957) observed fish concentrations during winter and spring in a heated discharge harbor on Kentucky Lake, Tennessee; threadfin shad were so abundant that they hampered boating by clogging the cooling systems of outboard motors. But even this example is somewhat confusing because threadfin shad also concentrated in the unheated inlet harbor, clogging the intake screens of the power plant's cooling system.

SIZE DISTRIBUTIONS OF AGE 0 FISHES IN THE STUDY AREAS OF LAKE MONONA

To determine if sizes of age 0 fishes differed among outfall and reference areas, lengths and weights were obtained from specimens collected during electrofishing surveys of 1968 and 1969. By comparing sizes of fish caught on successive sampling dates from each area, we hoped to ascertain whether or not young fishes of the outfall area grew at different rates or differed in condition relative to their counterparts in the reference areas.

Length-Frequency Distributions of Age 0 Bluegill, Yellow Bass, and Black Crappie

Adequate samples, generally of 20 or more fish, allowed interareal comparison of bluegill length distributions on several dates during summer and fall 1968 and summer 1969. Afternoon and evening distributions during 1969 were considered separately; only afternoon data from 1968 were available.

During summer 1969, enough age 0 yellow bass and black crappie were collected for interareal comparisons of length distributions. Data from afternoon and evening samples were pooled to establish, for each species, a single length-frequency distribution for each area on each date.

Length distributions of age 0 bluegill differed among outfall and reference areas. During afternoon in both 1968 and 1969, age 0 bluegill from the outfall area were generally longer than those from either reference area; RI and RII fish had similar length distributions (Fig. 9). Among the study areas, length-frequency distributions differed more consistently at their upper ends than at their lower ends. In both years, the 75th percentile and median lengths varied significantly among areas (Friedman two-way AOV; $p < 0.05$), but in neither year was there a significant difference among 25th percentile lengths (Friedman two-way AOV; 1968: $p = 0.10$; 1969: $p = 0.24$).

Median lengths of age 0 bluegill caught at night in 1969 differed from those obtained during afternoon (sign test; $p < 0.05$; Fig. 9b). After 29 July, RII fish taken at night had greater median lengths than those from OA and RI (randomization test; $p < 0.05$), which were similar in length. On each date in August, the median length of RII fish at night was greater or only slightly less than during the day, but median lengths of OA and RI fish were less at night by as much as 8 mm and in only one case (RI, 4 August) ever greater at night than during the afternoon. From 21 July to 21 August, median lengths of night-caught bluegill from OA scarcely changed, being 16 to 19 mm on every date. Similarly, after 29 July, there was little tendency for increase in median lengths of RI bluegill caught at night.

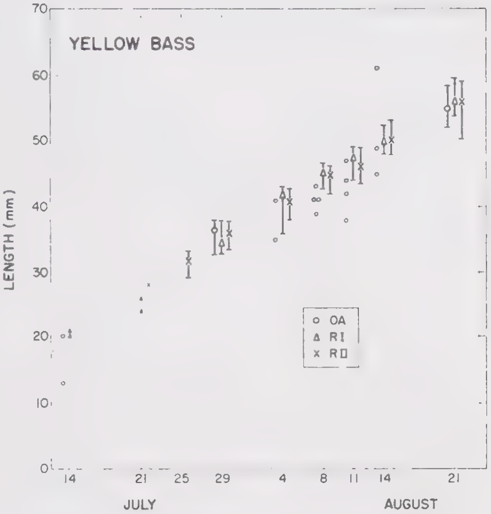


FIGURE 10.—Length-frequency distributions of age 0 yellow bass collected during afternoon and evening from each study area, 14 July–21 August 1969. Point symbols and vertical lines indicate the median and interquartile range for each sample of five or more fish. Smaller point symbols show lengths of individuals from samples of fewer than five fish.

Neither age 0 yellow bass nor age 0 black crappie were consistently longer in one area than in another during 1969 (Figs. 10 and 11). On 21 August 1969, the single date when more than 10 yellow bass were taken from each area, median lengths of fish from OA, RI, and RII did not differ significantly (extension of median test; $p = 0.75$). OA and RII supplied most of the age 0 black crappie caught during 1969. When median lengths of black crappie from OA and RII were paired by date from 14 July to 21 August (except 25 July when only two fish were caught in RII), application of the Wilcoxon test indicated no significant ($p > 0.05$) difference between areas.

Growth and movements.—The general increase in fish lengths as summer progressed (Figs. 9–11) was primarily the result of

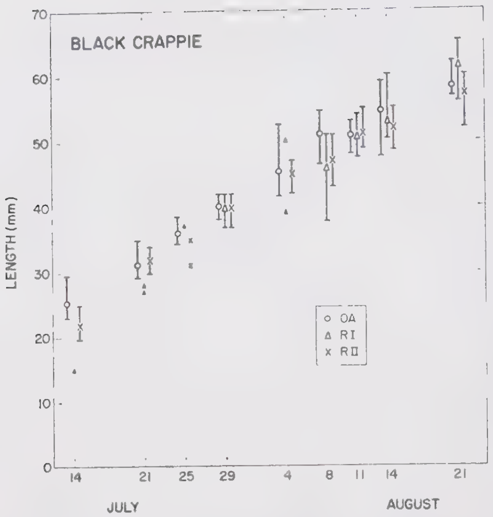


FIGURE 11.—Length-frequency distributions of age 0 black crappie collected during afternoon and evening from each study area, 14 July–21 August 1969. Point symbols and vertical lines indicate the median and interquartile range for each sample of five or more fish. Smaller point symbols show lengths of individuals from samples of fewer than five fish.

growth. Growth rates of age 0 fishes may have differed among areas, but any difference was obscured by other processes, particularly size-dependent movements of the fish.

At night, larger age 0 bluegill moved away from sampling locations in OA and RI to a greater extent than from those in RII. Because median lengths of fish from both OA and RI were less at night, movements perpendicular to shore rather than along shore were indicated. Diel onshore-offshore movements by larger bluegill fry have been postulated by Werner (1967). The smaller day-night difference in lengths of RII fish may have been related to the more gradual bottom slope in RII. Whatever the cause of apparent offshore movements, they were not directly related to operation of the power plant because it scarcely affected RI.

The apparent importance of size-differential movements on diel changes in age 0 bluegill length distributions suggested that persistent afternoon differences in fish lengths among areas were not entirely or even primarily due to interareal differences in growth rate. Larger age 0 bluegill may have been attracted to the outfall area from adjacent areas. Certainly, larger catches of age 0 bluegill from the outfall area than from reference areas implied active concentration of fish in the outfall area. It seems reasonable that larger fish, being more mobile than smaller fish, would have been differentially concentrated.

Comparison with age 0 fishes in other waters.—In no other system receiving thermal effluent have length distributions of age 0 fishes been investigated. However, data are available on rates of length increase for age 0 bluegill, yellow bass, and black crappie in unheated waters.

Median lengths of age 0 bluegill caught during afternoon from Lake Monona increased at rates commensurate with those observed for other populations, about 0.5 mm/day. Age 0 bluegill measured by Krumholz (1949) increased between 12 and 25 mm total length at 0.1 to 0.6 mm/day. Werner (1969) estimated that young bluegill grew 0.4 mm/day in an Indiana hatchery pond. But, on 14 August during both 1968 and 1969, age 0 bluegill from Lake Monona were 3–5 mm shorter than a 10-yr average computed for age 0 bluegill in Clear Lake, Iowa (Ridenhour 1960).

On 14 August 1969, Lake Monona age 0 yellow bass were about 5 mm shorter but age 0 black crappie about 5 mm longer than 10-yr averages for these species on 14 August in Clear Lake, Iowa (Ridenhour 1960).

Although the authors just cited have assumed that changes in average length of fish from date to date were due primarily to growth, their data, like those from Lake Monona, were potentially confounded by length-dependent recruitment, mortality, and movements of the fish.

Length-Weight Relationships of Age 0 Bluegill

Length-weight relationships of bluegill were examined for evidence of differences in condition between fish in outfall and reference areas. Specimens collected during four afternoons in 1968 and during afternoons and evenings on three dates in 1969 were removed individually from the preservative, blotted on a paper towel, weighed, and then measured. Weight and total length of each fish were

TABLE 2.—*Weight of age 0 bluegill from the outfall area relative to fish with the same length from reference areas. Values are mean ranks (see text) ranging between 1 and 2. A mean rank greater than 1.5 indicated that outfall fish were heavier than reference fish of same length*

	Mean rank						
	1968				1969		
Length (mm)	8 August	21 August	20 September	30 November	4 August	11 August	21 August
15–19	1.8	—	—	—	1.7	1.6	1.3
20–24	1.9	2.0	1.8	—	1.4	1.6	1.9
25–29	2.0	1.9	1.2	—	2.0	1.0	1.4
30–34	1.6	1.3	1.0	—	—	—	1.6
35–39	1.2	1.4	1.2	1.0	—	—	—
40–44	—	—	1.2	1.3	—	—	—
45–49	—	—	—	1.3	—	—	—

recorded to the nearest 0.01 g and 1 mm, respectively.

Median weights of fish in each 1-mm length class were determined for each of the three areas on each date. Medians for the two reference areas were averaged at each length, and the average was compared to the median for fish of the same length from the outfall area. If no fish of a particular length was caught from one reference area, the median from the other reference area was used as the basis for comparison. The reference and outfall-area values were ranked within each 1-mm length class, the larger value being assigned rank 2 and the smaller 1 (both 1.5 if tied). Ranks were then summed for each of several 5-mm intervals of length and an average rank within each interval was computed for the outfall area. Under an hypothesis of no difference between weights of outfall and reference-area fish of the same length, expected average ranks of outfall-area fish were 1.5 for all 5-mm length intervals on each date.

In both years, about half (7 of 17 in 1968; 6 of 10 in 1969) the averages exceeded the expected value (Table 2). However, in 1968, average rank and fish length were significantly associated (chi-square one-sample test; $p < 0.01$). Outfall fish smaller than about 30 mm were heavier than their counterparts from the reference areas; at greater lengths reference-area fish were heavier than those from the outfall area. The transitional length may have decreased through time from August to November. No consistent trend was evident in 1969; relative condition of outfall fish fluctuated erratically with fish length and date (Table 2).

Although condition of OA fish relative to those from the reference areas varied systematically in 1968, the difference between smallest and largest of OA, RI, and RII median weights at each length amounted to only about 6% of the smallest median weight. Differences of this magnitude must have resulted partly from systematic variation in tissue mass of fish with equal length and not totally from differences in gut content of fish having identical tissue mass. Stomach contents of age 0 bluegill from an adjacent lake constituted only 2% of whole fish weight (J. F. Kitchell, Laboratory of Limnology, University of Wisconsin, personal communication). In any event, condition of outfall age 0 bluegill was never very different from that of reference-area fish.

Strawn (1969) and Trembley (1965) noted that fishes (species and sizes not specified) living in heated discharge areas seemed to be in good condition. However, brown bullhead and white catfish (*Ictalurus catus*) living in an effluent discharge canal on the Connecticut River had significant losses of condition during winter (Merriman 1970).

TEMPERATURE DISTRIBUTIONS OF FISHES IN THE OUTFALL AREA DURING SUMMER

Catch/Effort with Respect to Water Temperature

To generally relate fish distributions within the outfall area to temperature, the catch/effort data collected during August 1968 and July–August 1969 were examined for association with water temperature. Catch from each electrofishing run in the outfall area was

TABLE 3.—*Number of electrofishing runs made in the outfall area during summer by temperature, year, and time of day*

Median run temperature (C)	Number of runs			
	August 1968		July–August 1969	
	Day	Night	Day	Night
33.5	1	1	—	1
33.0	1	—	—	—
32.5	2	1	1	—
32.0	—	4	2	3
31.5	4	1	8	4
31.0	4	1	7	4
30.5	—	—	2	6
30.0	3	3	7	6
29.5	3	4	4	7
29.0	3	2	5	3
28.5	5	2	1	4
28.0	—	3	3	2
27.5	1	5	2	1
27.0	—	1	3	2
26.5	3	1	2	1
26.0	—	1	—	2
25.5	—	—	1	1
25.0	—	—	—	1
All	30	30	48	48

assigned the median temperature recorded during the run (Table 3). The catch was then categorized by species, length-class, year, and time of day. For each category of catch, catch/effort at each 0.5 C increment of temperature was computed. The resulting temperature distributions of catch/effort were analyzed for nonuniformity by application of the Kolmogorov-Smirnov one-sample test, $p \leqslant 0.05$. This analysis enabled identification of those fishes that tended to be more abundant at some than at other temperatures.

Fishes occurred at virtually all available temperatures, but in several cases the distribution of catch/effort was significantly nonuniform with respect to median run temperature (Table 4). Among fishes inferred to be not equally abundant at all temperatures, only longnose gar and medium-sized yellow bass were biased toward temperatures higher than expected under the hypothesis of uniform distribution: The expected interquartile range of catch/effort at night in 1969 was 26.5–31.0 C, but interquartile ranges for longnose gar and medium-sized yellow bass were 30.0–32.0 C and 28.5–31.0 C, respectively. Small rock bass, large pumpkinseed, small bluegill, largemouth bass, small black crappie, and small yellow perch were distributed at temperatures lower than expected; the same pattern held for large carp during the day in 1968 and for large and medium-sized bluegill at night in 1969. Small carp were concentrated at temperatures near 29 C during both day and night in 1969.

Gammon (1971) and Proffitt (1969) investigated near-outfall distributions of fishes belonging to faunas similar to that of Lake Monona. Although neither worker estimated the relative abundances of fishes at various temperatures, both concluded that most fishes avoided temperatures exceeding 33–34 C. On sampling dates in 1968 and 1969, only water in the jets and very near the outfalls of Lake Monona consistently reached 33 C. But several fishes, particularly smaller individuals, were relatively scarce above 30 C. Lowered abundance at higher temperatures may have resulted partly from avoidance of strong currents near the jets where higher temperatures occurred.

Fine-scale features of the temperature distributions of OA fishes were obscured by the large scale of sampling. Variation of temperature within a run limited resolution of capture temperatures to about 4 C. Fish caught at all points along a transect were assigned the median run temperature, but a fish caught near an end of some transects (Op, for example) may have been at temperatures 2–4 C lower or higher than the median. Median run temperatures overestimated temperatures experienced by fish that stayed near the bottom, because bottom temperatures were usually lower than at 0.5 m where temperature was recorded.

Most studies of heated discharge sites have generally yielded inadequate data on the temperature distributions of fishes (Coutant 1970). This has largely resulted from inability to measure, reliably and simultaneously, (1) water temperatures where fishes actually live, and (2) relative abundances of fishes within an area reasonably homogeneous except for variation in temperature. Allen, Boydstun, and Garcia (1970), for example, caught marine fishes by hook and line in the discharge area of a power plant at Buhne Point, California. Because it was impractical to measure temperatures at the points where

Table 4.—*Temperatures below which were obtained—and temperatures below which were expected—25%, 50%, and 75% of catch/effort from the outfall area during summer (see text). Each observed distribution of catch/effort that differed significantly from the expected distribution (uniform) is indicated by underlined quartile temperatures. Number of fish (N) contributing to each observed distribution appears to the right of the third quartile temperature*

		August 1968								July–August 1969							
		Day				Night				Day				Night			
		Quartile temperature (C)				Quartile temperature (C)				Quartile temperature (C)				Quartile temperature (C)			
Species	Length (mm)	1st	2nd	3rd	N	1st	2nd	3rd	N	1st	2nd	3rd	N	1st	2nd	3rd	N
Longnose gar	>350	—	—	—	—	—	—	—	—	—	—	—	—	30.0	31.0	32.0	25
Carp	≤150	—	—	—	—	—	—	—	—	29.0	29.5	30.0	14	28.5	29.0	30.0	17
	>150	26.5	29.5	30.0	11	28.0	29.5	31.5	23	—	—	—	—	27.0	30.0	31.0	14
Yellow bass	51–100	—	—	—	—	—	—	—	—	—	—	—	—	28.5	30.5	31.0	14
	>100	—	—	—	—	27.5	30.0	31.5	13	28.0	29.5	31.5	10	26.0	30.0	31.0	29
Rock bass	≤50	—	—	—	—	—	—	—	—	27.5	29.0	29.0	44	26.0	28.5	28.5	14
Pumpkinseed	≤75	28.5	30.0	32.0	31	28.5	29.5	32.0	15	—	—	—	—	—	—	—	—
	>75	—	—	—	—	—	—	—	—	—	—	—	—	25.0	29.5	30.0	20
Bluegill	<75	27.0	29.0	31.0	3,681	27.0	29.0	30.5	1,940	26.5	28.5	29.0	838	26.0	28.5	29.5	634
	76–100	28.0	31.0	33.0	11	27.0	28.5	30.5	15	28.5	29.0	30.0	25	26.5	27.0	30.0	22
	>100	29.0	29.5	33.5	17	27.0	30.0	32.5	37	—	—	—	—	26.0	27.0	29.5	82
Largemouth bass	>50	—	—	—	—	—	—	—	—	25.5	28.0	29.5	24	—	—	—	—
Black crappie	≤75	26.5	29.0	30.0	24	—	—	—	—	26.5	27.0	28.5	76	26.0	27.5	29.5	55
Yellow perch	26–100	—	—	—	—	—	—	—	—	25.5	27.5	30.5	11	—	—	—	—
Expected distribution (uniform)		28.5	30.0	32.5		27.5	29.3	31.5		27.5	29.3	31.0		26.5	28.8	31.0	

fishes were taken, catches could only be classified as coming from water warmer or cooler than 10.5 C.

Body Temperatures of Fishes with Respect to Water Temperature

The analysis of catch/effort provided a coarse measure of the temperatures experienced by fishes in the outfall area. During summer 1970, body temperatures of just-caught specimens were measured to obtain more accurate definition of fish distributions with respect to temperature. Sampling effort was expended during afternoon and evening on 11, 13, 17, 19, and 21 August 1970 throughout the outfall area.

Fishes were caught by the electrofishing technique described above, except that stunned individuals were removed from the water by hand-held dip net. After each specimen was lifted from the water, its body temperature was measured within 40 sec (median time, 12 sec) and recorded along with total length of the fish, central standard time, 0.5-m water temperature, and water depth.

Body temperatures were measured with a thermistor-bridge circuit. The thermistor, fixed in the tip of a 16-gauge hypodermic needle, was inserted into the epaxial musculature beneath the dorsal fin of the fish to a point near the interneural spines. The temperature measuring system reached thermal equilibrium within 3 sec.

Body temperatures of most fishes tended to increase with water temperature (Fig. 12). However, the slope of the relationship between fish and capture temperature was generally less than unity, i.e., fish temperatures tended to vary less than water temperatures. Body temperatures of yellow bass, rock bass, and yellow perch were virtually independent of capture temperatures.

Some fishes had body temperatures consistently higher than those of others caught during the same diel period (Fig. 13). Bluegill longer than 100 mm, largemouth bass longer than 100 mm, carp, and pumpkinseed had median body temperatures above 30 C during the afternoon; in contrast, afternoon medians for yellow bass, black crappie, rock bass, and yellow perch were below 29 C. Ex-

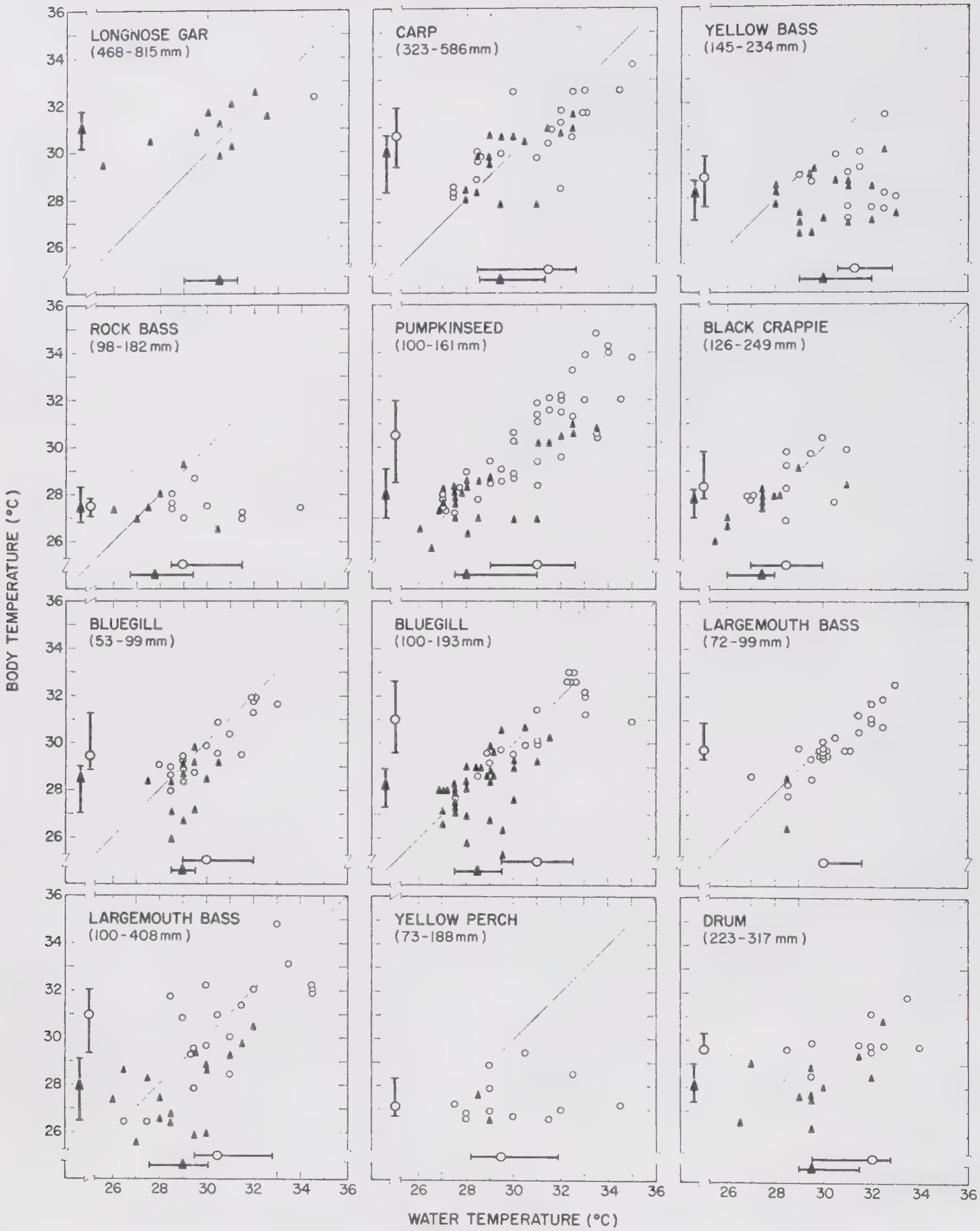


FIGURE 12.—Body temperature of fish and water temperature (0.5 m depth) at the place of capture for each fish caught in the outfall area during afternoon (open circle) and at night (filled triangle), August 1970. Distributions of body and water temperature are summarized near the respective axes by medians (large open circles and filled triangles for afternoon and night, respectively) and interquartile ranges (lines extending from medians).

cept for longnose gar and carp, with median body temperatures of 31.0 and 29.8 C, respectively, median fish temperatures at night were between 28.4 and 27.8 C, being highest for smaller bluegill and lowest for rock bass.

At night, both fish and 0.5-m temperatures were lower than in the afternoon; in fact, sample medians were lower at night in every case. Comparison of 95% confidence intervals for the medians indicated that body temperatures of five species at night were significantly lower than during the afternoon—bluegill, largemouth bass, pumpkinseed, black crappie, and freshwater drum. However, median water temperatures at points of capture decreased significantly from afternoon to night only for larger bluegill and for pumpkinseed.

Intramuscular temperatures depended primarily on the environmental temperatures a fish experienced during some short time interval (probably less than 30 min), ending at the moment of capture. Two other sources of variation may have influenced body temperatures: metabolic heat production and thermal exchange with the environment after capture. Because of muscular thermogenesis, core temperatures of fishes can exceed the temperature of the water in which they live (Barrett and Hester 1964; Carey and Teal 1969a, 1969b; Stevens and Fry 1970). Only active large fishes such as tunas and pelagic sharks maintain body temperatures several degrees warmer than their environment, but even *Tilapia mossambica* weighing only 40 to 200 g were about 0.5 C warmer than the 22–24 C water bath in which Stevens and Fry (1970) kept them. Larger fishes we caught, such as 5- to 8-kg carp, probably had body temperatures no more than 1 C above ambient temperature. Change in body temperature from the time a fish was stunned until its temperature was measured probably amounted to less than 0.5 C, even for smaller specimens. Despite the two sorts of potential error, intramuscular temperatures probably estimated within 1 C the exponentially smoothed average of each specimen's "recent" thermal experience.

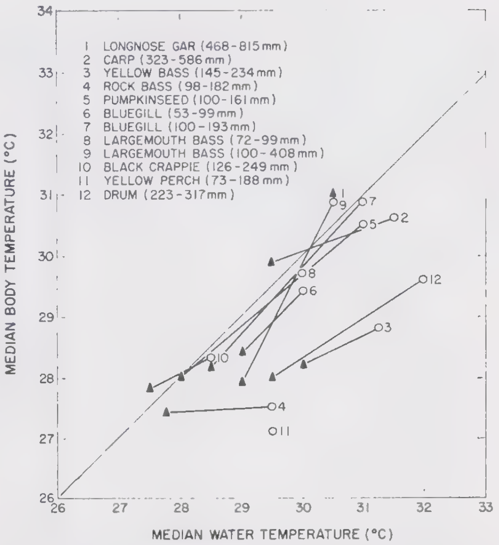


FIGURE 13.—Median body temperature of fish and median water temperature (0.5 m depth) at the places of capture for each of 10 species of fishes caught in the outfall area during afternoon (open circle) and at night (filled triangle), August 1970. This figure summarizes data from Figure 12.

Body temperatures were a better measure than capture temperature of where in the thermal environment fish actually lived. Variation of water temperature with depth rendered capture temperature a poor estimator of the temperatures experienced by some fishes, particularly those that lived near the bottom—yellow bass, rock bass, yellow perch, and freshwater drum (Fig. 13). Yellow bass, which concentrated near the discharge jets, actually lived in relatively cool water near the bottom. In contrast, longnose gar spent much of their time near the surface at temperatures higher than those recorded at 0.5 m. Several individual longnose gar, carp, and largemouth bass were 1–3 C warmer than the water from which they were caught (Fig. 12); these fishes must have moved horizontally from warm water into cooler water just prior to capture. Similarly, relatively low body temperatures of some specimens taken in the outfall area (particularly at night) suggested recent emigration from cool, deep water outside the outfall area.

The nocturnal decrease in both body temperatures of fish and water temperatures where they were caught was attributable to several causes:

(1) The outfall area in general was about 1.5 C cooler at night than in the afternoon.

Thus, had the fish simply maintained the same spatial distributions at night as during the day, they would have been cooler at night. However, median body temperatures of large bluegill, large largemouth bass, and pumpkinseed were more than 2.5 C lower at night than during afternoon, differences too large to have been produced wholly by nocturnal cooling of the outfall area without changes in fish distribution.

(2) Some fishes moved away from the jets into cooler water at night; large bluegill exhibited this distributional pattern. Young largemouth bass were abundant near the jets, particularly Js, during the afternoon, but they were rarely encountered anywhere in the outfall area at night.

(3) Some fishes may have stayed nearer the bottom at night than during the day. Adult largemouth bass and pumpkinseed were occasionally seen resting inactively on or just above the bottom at night; both species swam at mid-depths during afternoon. Even in water only 1 m deep, a fish that descended from 0.5 m to the bottom could have encountered temperatures as much as 3 C lower (Fig. 4).

(4) Decreased body temperatures at night could have resulted from a nocturnal increase in the rates at which fish swam into and out of the outfall area. Fishes swimming into warmer water of the outfall area would have warmed gradually at rates inversely proportional to body size. If results obtained by Stevens and Fry (1970) for *Tilapia* are applicable to the similarly proportioned bluegill, a 150-g fish (about 190 mm long) would have warmed to only 29 C six min after it had moved from 25 C water into 30 C water. In theory, then, recent immigrants would have had lower muscle temperatures than fish that had lived at the same elevated temperatures for a longer time. It is unlikely, however, that any nocturnal increase in fish movements could have been so drastic as to have shortened average residence times to the requisite level, ca. 10 min or less.

Therefore, that fish and capture temperatures were lower at night than during the day is attributed primarily to (1) a general decrease in temperature of the outfall area at night, (2) movements of fishes away from the jets at night, and (3) a tendency for fishes to stay nearer the bottom at night. Whereas processes (1) and (2) would have lowered both fish and capture temperatures, process (3) would have caused reduction in fish temperatures but not capture temperatures.

With the exception of Trembley (1960), other students of temperature distributions of freshwater fishes have not measured body temperatures but have relied instead on water temperatures measured where fishes were caught. Trembley measured gut temperatures of fishes caught in the outfall area of a power plant on the Delaware River, Pennsylvania. Fishes were caught by seining or hook and line; then, a mercury thermometer was inserted into the stomach by way of the mouth or anus. Although few data were presented for fishes living in the discharge lagoon, gut temperatures were graphed for about 50 fishes caught during June by hook and line approximately 500 m downriver from the discharge point. Brown bullhead and smallmouth bass were about 21–23 C (normal river temperature) during early morning before the power plant came on load, but gut temperatures of brown bullhead, smallmouth bass, and white catfish caught during midafternoon were 27–32 C. No river temperatures were given for the fishing location, but the effluent temperature was 39 C.

Temperature Acclimation Levels of Age 0 Bluegill

Age 0 bluegill were by far the most abundant group of fishes in the littoral zone during summer. However, no data on their temperature distribution were provided by the survey of body temperatures because small body sizes precluded effectual measurement of internal temperatures. Therefore, to evaluate the temperatures experienced in the outfall area by age 0 bluegill, we estimated their levels of temperature acclimation by heat resistance tests.

Young bluegill, 20–70 mm long, were caught by 10- to 20-m-long runs with the push net (no electroshock) from locations at both sides of both jets. One sample of 50–60 fish was obtained from each of the four locations during early afternoon on each of five successive dates, 31 August–4 September 1970.

The fish were transported to the laboratory and held overnight in styrofoam containers filled with Lake Monona water from outside the outfall area. During this time, the water temperature in the containers changed from 23–26.5 C to ambient temperature in the laboratory, 21.5–24.0 C. The thermal experience of the fish after capture was always at or below the minimum temperature recorded at capture.

On the day following capture, about 20 fish from each sample were transferred to a lethal temperature bath at 36.5 ± 0.05 C. Each bath contained 25 liters of continuously aerated water from Lake Mendota (which discharges into Lake Monona through a 1.3-km segment of the Yahara River). Resistance time, i.e., the time between entry into the bath and death (cessation of gill movement), was recorded for each specimen.

To relate resistance times of fish from the outfall area to their level of temperature acclimation, the resistance time distributions for age 0 bluegill of known temperature acclimation were required. For this calibration, about 400 age 0 bluegill were collected from RII with several short runs of the push net (no electroshock) on the afternoon of 16 September 1970. Water temperature 0.5 m beneath the surface was 20 C. The fish were transported in styrofoam containers to the laboratory where half were put into each of two acclimation tanks; each tank contained 100 liters of continuously aerated and filtered Lake Mendota water at 22 C. Fifteen hours later the temperature of each tank was reset for 26.0 C. After 30 hr at 26.0 C, one tank was raised to 30.0 C; the other tank remained at 26.0 C. After 3 additional days, fish in the two tanks were assumed to be fully acclimated to temperatures at least as high as 26.0 and 30.0 C. Fish were randomly withdrawn from each tank for determination of their distributions of resistance time. As soon as the samples had been removed, the temperature of each acclimation tank was increased 1.0 C. On subsequent days, the temperature of each tank was increased a maximum of 1.0 C per day. Fish acclimated to 26.0, 27.0, 28.0, 29.0, 29.5, 30.5, and 31.0 C were tested from one tank; fish acclimated to 30.0, 31.0, 32.0, and 33.0 C were tested from the other. Temperatures in each acclimation tank varied less than 0.1 C about the set points.

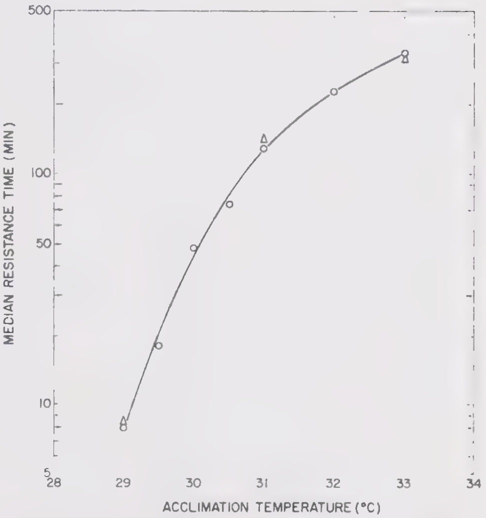


FIGURE 14.—Relationship of acclimation temperature and median time to death at a lethal temperature (36.5 C) for samples of 20 age 0 bluegill acclimated in the laboratory. Circles indicate samples held overnight at room temperature before resistance tests; triangles indicate samples tested immediately after removal from the acclimation temperature. The curve, fitted by eye to the circles, was used to estimate acclimation temperatures of fish from the outfall area (Fig. 15).

During acclimation, the fish experienced a 14-hr light period each day (0600–2000 CST) followed by 10 hr of darkness. Light was supplied by a 15-watt incandescent bulb centered about 15 cm above the surface of each tank. Photoperiod control circuitry provided "dawn" and "dusk" periods of about 1 hr (see p. 692).

The fish were fed at least once daily with living zooplankton, primarily *Daphnia* sp. from Lake Monona or Lake Mendota.

Fish were removed from the acclimation tanks about 0.5 hr after feeding, held overnight in styrofoam containers at ambient temperature (21–23 C), and then tested in the same manner as the fish of unknown acclimation. To determine whether substantial loss of acclimation occurred during overnight holding at ambient temperature, additional

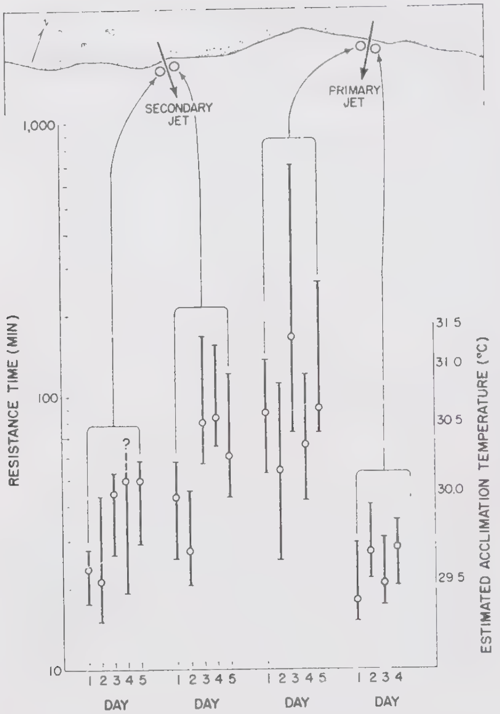


FIGURE 15.—Median (circle) and interquartile range (vertical line) of times to death at a lethal temperature (36.5 C) and estimated median acclimation temperature (circle) for each sample of about 10 age 0 bluegill from the outfall area, 31 August–4 September 1970. The data from each sample are grouped by location of sample collection and ordered within each group by date of sample collection (day 1 = 31 August, . . . , day 5 = 4 September).

samples were tested immediately after removal from the acclimation tanks.

With the relationship between acclimation temperature and resistance time established (Fig. 14), we could proceed with evaluation of heat resistance data on age 0 bluegill tested directly from the outfall area.

Median times of heat resistance, ranked within dates, varied significantly among locations within the outfall area (Friedman two-way AOV; $p < 0.02$). Young bluegill collected between the two jets had longer resistance times than their counterparts caught on the same date from outside the respective jets (Fig. 15). Fish from each side of the primary jet differed more in heat resistance than those from each side of the secondary jet. Data from all locations and dates indicated that

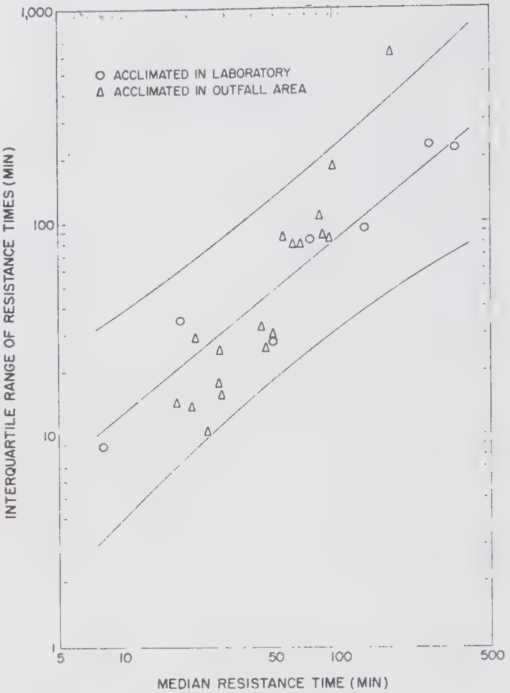


FIGURE 16.—Interquartile range of resistance time related to median resistance time for samples of age 0 bluegill acclimated to constant temperatures in the laboratory or collected from the outfall area. The middle line indicates the least-squares linear regression of log interquartile range on log median resistance time for laboratory-acclimated fish; the upper and lower lines bound the 95% parametric confidence interval about the regression line.

median heat resistance times were positively correlated (Kendall's $\tau = 0.44$; $p < 0.01$) with water temperature at the sites of fish collection. Water temperature within locations differed significantly among dates (Friedman two-way AOV; $p = 0.05$); median resistance times did not (Friedman two-way AOV; $p = 0.25$).

All samples of fish from the outfall area had median resistance times corresponding to those of fish acclimated between 29.4 and 31.3 C in the laboratory (cf. Figs. 14 and 15). Water temperatures at fish-collecting sites ranged from 25 to 36 C. Thus, age 0 bluegill at different locations in the outfall area were acclimated to temperatures constituting a narrow interval in the range of available habitat temperatures. Moreover, individual fish within each location were apparently acclimated to virtually the same temperature, because variation of resistance times within samples of fish from the outfall area did not differ greatly from variation within samples of homogeneously acclimated fish having corresponding median resistance times (Fig. 16).

Although all samples of bluegill from the outfall area had estimated acclimation temperatures within a 1.9 C interval, the four locations nevertheless yielded differently acclimated fish. The difference in acclimation between fish from the two sides of each jet implied that age 0 bluegill did not freely mingle across the jets, particularly the primary jet. The continuous, high velocity discharge from the primary outfall probably constituted a more effective barrier to alongshore movements of young bluegill than did the intermittent, diffuse flow from the secondary outfall.

Heat resistance of young bluegill from the outfall area was assumed to vary only with the time-temperature distribution they experienced up to the time of capture. Precise inferences about the distributions were not permitted by the heat resistance data because a given level of heat resistance could have resulted from any number of sequential combinations of temperature and exposure time.

However, evidence from the literature suggested that most thermal experience accumulated by the fish during the several days prior to capture occurred at or below the estimated acclimation temperature. Acclimation levels of brown bullhead in a small Ontario lake during summer were more similar to maximum (25–26 C) than to average (18–22 C) water temperatures (Brett 1944). Cutthroat trout (*Salmo clarki*) kept constantly at 20 C and at temperatures that cycled (square wave) from 10 to 20 C every 6 to 48 hr were almost equally heat tolerant (Heath 1963). Female mosquitofish (*Gambusia affinis*) in an experimental temperature gradient spent most of their time between 25.5 and 29 C, and the mean temperature of their distribution was about 27 C (Bacon, Neill, and Kilambi 1968). Even so, they were more heat resistant than fish acclimated to 28 C and probably had an average acclimation level of about 29 C (cf. Hart 1952).

If young bluegill in the outfall area behaved like the mosquitofish in their heterothermal environment, they probably spent most of the time at temperatures lower than their estimated acclimation temperatures. Periodic decreases in temperature within the outfall area (Fig. 3) would not have resulted in greatly decreased heat resistance levels because acclimation to a lower temperature occurs slowly (Brett 1944, 1946). Median resistance times of acclimated bluegill held overnight at temperatures 10 C below the acclimation temperature differed little from those of fish tested immediately after removal from the acclimation tank (Fig. 14).

Proximity of fishes' acclimation levels during summer to maximum habitat temperatures (and the persistence of attained levels despite drops in environmental temperature) Brett (1944) attributed to "a 'summation' in temperature adaptation in a field of varying temperatures." Summation, in Brett's usage, occurs because fishes' loss of tolerance to high temperatures proceeds slowly compared with rates of upward acclimation (Loeb and Wasteneys 1912; Brett 1944, 1946; Heath 1963). In habitats having upper or lower temperatures so extreme that fish avoid them, summation occurs only over the range of temperatures actually encountered and results in eventual acclimation to the temperature demarcating the limit of upper avoidance temperatures. Our data indicated that the upper limit for young bluegill in the outfall area was no higher than about 31.5 C.

BEHAVIORAL REGULATION OF TEMPERATURE BY FISHES IN THE LABORATORY

Introduction

To evaluate the extent to which temperature might govern distributions of fishes in the outfall area of Lake Monona, thermoregulatory behavior of representative species was investigated in the laboratory.

Temperatures preferred by fishes were determined by allowing specimens to behaviorally regulate the temperatures of tanks in which they lived; the experimental approach has been described by Neill, Magnuson, and

Chipman (1972). Temperature preference data were collected from young fish representing six species that differed among themselves in the temperatures at which they occurred during summer in the outfall area.

With additional experiments on two of the six species, we explored the behavior of fish in environments with food available at only one of two temperatures. The object of these experiments was to determine the extent to which fish might invade water warmer or cooler than the preferred temperature to get food.

General Equipment and Procedures

Each of 10 test tanks was a 50-liter fiber glass aquarium with one glass side; inside dimensions were 60 cm long × 30 cm wide × 30 cm deep. A double-walled partition of black (opaque) Plexiglas divided each tank into halves. A tube (40 mm inside diameter) of black polyethylene penetrated the center of the partition to form a 6-cm-long tunnel through which a fish could swim from one half of the tank into the other.

An electronic monitoring system sensed and recorded the time and direction of each pass of a fish through a tunnel. Sensing elements of each test unit were a pair of photocells in waterproof glass tubes. The photocells received light passing horizontally across the tunnel from a pair of light sources (red, about 6,500 Å) mounted in tubes that penetrated the tunnel's opposite wall. Interruption of a light beam by a fish caused a voltage drop through the photoelectric cell which, when amplified by transistors, produced a change in state of a bistable multivibrator. State of the multivibrator and its signal to an event recorder were determined by which light beam (right or left member of the pair) was last interrupted. Whether a fish passed completely through the tunnel or only entered the tunnel to then back out into the same side of the tank, the result of the action was correctly interpreted: After the move, the fish was in that half of the tank adjacent to the light beam last broken. A second channel of the event recorder was activated whenever either or both light beams were blocked, whether or not a change occurred in state of the multivibrator. The two channels together provided a continuous, unambiguous, and permanent record of a single fish's movements between the halves of each tank through time.

Each half of each test tank was supplied with the following basic equipment: (1) a compressed air diffuser for aerating and mixing the water; (2) one or more submersible aquarium heaters switched by a mercury contact thermometer through a solid state relay to precisely maintain above-ambient temperatures; (3) a coil of acrylic-coated copper tubing through which cold water could circulate to decrease ambient temperature; (4) a 0.5-liter polyethylene bottle (with holes, and the top half removed) which contained the cooling coil, heaters and air diffuser—an arrangement that increased the efficiency and precision of temperature control; (5) a truncated tetrahedron of clear, 3-mm-thick Plexiglas panes that formed a "funnel," the smaller end of which surrounded the mouth of the tunnel to facilitate location of the tunnel by the fish, especially during darkness; and (6) a 0.5-liter glass jar covered with black polyethylene film and laid on its side at the bottom of the tank to provide cover for the fish.

Except during tests, experimental fishes lived in 30- to 200-liter holding tanks. Submersible heaters switched by contact thermometers through solid state relays enabled precise (±0.1 C) control of temperature in some holding tanks. Other tanks had no temperature control equipment and fluctuated with ambient temperature (18–23 C). Cooling coils were not used in holding tanks.

The test and holding tanks were in a chamber fabricated from a wooden frame covered with black polyethylene film to exclude extraneous light. Each tank was illuminated by an incandescent bulb centered 15 cm above the water. The test tanks and 30- and 50-liter holding tanks were lighted by 15-watt bulbs; a 25-watt bulb lighted the single 200-liter holding tank. Illumination was controlled by capacitor-dimmer circuitry coupled to a 24-hr timer to provide a 14:10 photoperiod (the 1 August photoperiod at Madison) with "dawn" between 0600 and 0700 and "dusk" between 2000 and 2100 CST.

Only filtered (otherwise untreated) Lake

Mendota water was used in all tanks. Water in each tank was continuously aerated. Some water from each tank was exchanged for fresh water at least once every week for holding tanks, or once every 3 days for test tanks.

Maintenance of Environmental Temperature by Behavioral Thermoregulation

Experimental Technique and Procedures.—Eight of the 10 test tanks were modified to evaluate thermoregulatory performances of young fishes through the technique described by Neill, Magnuson, and Chipman (1972). The left-right signal from the monitor unit of each tank controlled heat transfer so that a fish could regulate temperature by dividing its time between halves of the tank. Passage of the fish into one side (e.g., right) of the tank caused that side to begin warming at 3 to 5 C an hour. Warming of the right side ceased only when the fish swam to the other side; then the right side began cooling at 3 to 5 C an hour. Temperature of the left side was kept 2 C lower than that of the right side by a comparator-relay circuit. Accordingly, the fish always had available alternative temperatures 2 C apart within the range 18–40 C. Sequential testing and choosing of one temperature over the other resulted in thermoregulation; thus, the fish served as its own thermostat.

In these experiments, a fish could maintain tank temperature in a "band" no narrower than 2 C, the differential between the two sides of the tank. A differential of 2 C was chosen for several reasons. In preliminary experiments in which the sides of a tank were set at constant temperatures 1 or 2 C apart, selection of one side over the other by bluegill and black crappie was more consistent when the difference was 2 C. This result was congruous with the observation by Moss (1970) that juvenile American shad (*Alosa sapidissima*) responded consistently to rapid temperature changes of 4 C but not to 1 C changes. A differential of 2 C was also more compatible with intrinsic comparator limitations than were smaller or larger differentials. Finally, larger differentials were difficult to manage because of heat flux problems.

Most young fishes placed in the tanks learned to swim through the tunnel within a few hours. During a training period of 3 to 7 days, maximum attainable temperature of the warmer side was limited to 22 C. On the last day of training, maximum attainable temperature of the warmer side was advanced to 30 C and then, 24 hr later, to 40 C. During all experiments, temperature of each side of each test tank was recorded from a thermistor once every 6 min by a multi-channel analog recorder.

The thermoregulatory performance of each subject was assessed from data collected on the second, third, and fourth days after maximum attainable temperature was set at 40 C. The temperature record for each fish was divided into day (0700–2000) and night (2100–0600) categories. For each diel period, upper and lower turnaround temperatures were tabulated for the 3-day trial. Upper turnaround temperatures were local temperature maxima recorded from the warmer side of the tank; lower turnaround temperatures were the local minima recorded from the cooler side of the tank (Neill, Magnuson, and Chipman 1972). If a subject made fewer than three passes through the tunnel during a day or night period, turnaround temperatures for that period were excluded from analysis.

Species tested were carp, rock bass, bluegill, largemouth bass, black crappie, and yellow perch. Carp were seined in October 1969 from an oxbow of the Wisconsin River, 20 km below Prairie du Sac-Sauk City, Wisconsin. Black crappie and largemouth bass were seined from Lake Mendota on 21 April and 23 August 1970, respectively. All other specimens were caught by seine or push net from Lake Monona between 15 August and 15 September 1970. All specimens were less than 1 year old when they were collected.

Thermoregulatory tests began on 6 August 1970 and ended 20 November 1970. Largemouth bass were placed in the test tanks the day after capture. All other specimens lived in the holding tanks at ambient temperature (20–22 C) for at least 15 days prior to tests. Carp and black crappie, both kept under uncontrolled light conditions for several months after capture, lived in the experimental light environment for more than 30 days before they were tested. Total lengths of specimens at the end of tests were carp, 81–97 mm; rock bass, 48–59 mm; bluegill, 53–83 mm; largemouth bass, 65–75 mm; black crappie, 75–88 mm; and yellow perch, 82–118 mm. The numbers of fish tested were 5 carp, 6 rock bass, 13 bluegill, 8 largemouth bass, 8 black crappie, and 17 yellow perch.

Fishes were fed once daily during holding and training and twice daily during thermoregulatory tests. Carp, bluegill, and yellow perch were fed pelleted food; black crappie were fed mealworms (*Tribolium* spp.); largemouth bass were fed small fishes. Rock bass ate pellets and mealworms in the holding tanks but received only pellets in the test tanks. Food was put into that side of each test tank in which the fish occurred at the moment of feeding.

Results.—Regulatory performance varied with species, individual specimen, and time of day. Sample records have been presented by Neill, Magnuson, and Chipman (1972). In terms of amount of temperature fluctuation allowed by individual fish, bluegill were the best regulators, yellow perch poorest, and the others intermediate. The specimen that kept its environmental temperature most nearly constant was a bluegill: On the first day of the trial, it kept the warmer side of the tank between 31.5 and 32.0 C from 0600 to 1400, between 31.7 and 33.0 C from 1400 to 1700, and between 32.2 and 32.5 C from 1700 to 2000.

Each species maintained its environmental temperature between limits different from those observed for one or more of the other five species (Fig. 17). Carp and bluegill performed similarly; both species maintained temperatures between 28.5 and 33.5 C. Largemouth bass regulated at temperatures lower than carp and bluegill but somewhat higher than rock bass and black crappie, both of which avoided temperatures lower than 25.5 C or higher than 30.0 C. Yellow perch avoided temperatures higher than 26.5 C; they kept their environment decidedly cooler than did any other species.

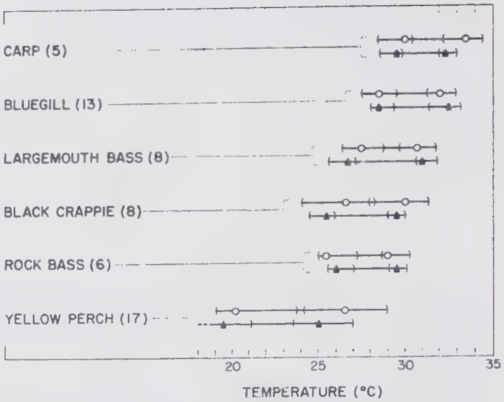


FIGURE 17.—Upper and lower turnaround temperatures for thermoregulating carp, bluegill, largemouth bass, black crappie, rock bass, and yellow perch. Medians during day and night are indicated by open circles and filled triangles, respectively. Parentheses about medians indicate the interquartile range of turnaround temperature. The number of fish tested is given in parentheses to the right of each species' name.

Whether or not yellow perch entered into the analysis, the species differed significantly among themselves in both upper and lower turnaround temperatures (Kruskal-Wallis one-way AOV; $p < 0.01$). Differences in regulatory performance among species were also supported by consideration of 95% confidence intervals constructed for median upper and lower turnaround temperatures (Neill 1971). Considering both day and night data and ignoring overlaps that were "small," a multiple-comparison test of confidence regions indicated the following groupings of the six species (in descending order from those regulating at highest temperatures):

1. carp ≅ bluegill ≅ largemouth bass;
2. largemouth bass ≅ rock bass ≅ black crappie;
3. yellow perch.

The exact probability level (Type I error) associated with the test could not be determined; it was probably somewhat greater than 0.05. (Problems relevant to multiple-comparison tests are discussed by Steel and Torrie 1960.)

A preferred temperature range could be defined for each species: the region of temperature bounded by the median upper and lower turnaround temperatures. The preferred temperature range for yellow perch was about 6 C wide. For the other five species, it was almost constant in width, about 3.5 C.

For no species was there a significant difference between day and night medians of either upper or lower turnaround temperature. However, the *variation* among regulatory performances of conspecific individuals did change from day to night; in each species, upper as well as lower turnaround temperatures were less variable at night than during the day (Fig. 17).

Activity, as measured by the frequency of tunnel passes, varied among species and, within species, between day and night (Table 5). Species maintaining highest temperatures were also most active. Never did any carp or largemouth bass, and only once did a bluegill or a rock bass, make fewer than 10 tunnel passes during 1 day or night; usually, each fish passed through the tunnel more than 10 times during each hour. The event records indicated that rock bass were more active than black crappie; however, the two species differed less in the proportion of cases in which fewer than 10 passes were made per period (Table 5). Yellow perch were less active than any other species. In several cases, yellow perch made few or no passes through the tunnel during the night (Table 5). Individuals of the other species made frequent tunnel passes after dark, although activity was reduced at night.

Discussion.—Activity level and thermoregulatory performance were not independent of each other. More active fish, for example bluegill, kept their environment warmer than did less active fish like yellow perch. Whether activity and thermoregulation were related as cause and effect, or effect and cause, could not be determined. However, lowered nighttime activity did not result in significant decreases in the median turnaround temperatures, even though the frequency distribution of temperature between the turnaround points probably shifted toward lower temperatures. (Lack of synchronization between event and temperature records often made it impossible to determine which temperature of a pair the fish experienced at any instant; therefore, frequency distributions of temperature could not be constructed.)

TABLE 5.—*Frequency distribution of tunnel passes by thermoregulating fish. Total of the cases in each row equals the number of specimens multiplied by 3, the number of test days*

Species	Diel period	Number of tunnel passes per diel period										
		0	1	2	3	4	5	6	7	8	9	≥10
Carp	day	—	—	—	—	—	—	—	—	—	—	15
	night	—	—	—	—	—	—	—	—	—	—	15
Bluegill	day	—	—	—	—	—	—	—	—	—	—	39
	night	—	—	—	—	—	—	—	—	1	—	38
Largemouth bass	day	—	—	—	—	—	—	—	—	—	—	24
	night	—	—	—	—	—	—	—	—	—	—	24
Black crappie	day	—	—	—	1	—	—	—	—	1	—	22
	night	3	1	—	1	—	—	—	—		—	19
Rock bass	day	—	—	—	—	—	—	—	—	—	—	18
	night	1	—	—	—	—	—	—	—	—	—	17
Yellow perch	day	3	—	2	—	—	—	—	—	1	—	45
	night	16	2	5	2	1	—	—	—	2	—	23

That median turnaround temperatures at night were less variable than those during the day could be attributed to decreased intensities of nonthermal stimuli at night or decreased tendency for fish to respond to nonthermal stimuli at night. In any case, position effects apparently decreased at night so that individuals of each species responded to temperature more homogeneously at night than during the day.

The minimum possible width of the preferred temperature range was intimately related to activity of fish and to rate of heat exchange in the experimental system. The following equation approximated the relationship:

$$W = (r/f) + 2\,C$$

where, W = minimum width of range in degrees Celsius;
r = rate of temperature change;
f = frequency of tunnel passes.

Thus, to maintain a range width of 6 C in a tank whose temperature changed 4 C/hr, yellow perch must have moved at least once per hour. The other species, to maintain range widths of about 3.5 C, had to move at least 2.7 times per hour. Because many fish moved more frequently than 10 times per hour, temperatures could have been regulated more precisely than they were.

Turnaround temperatures were probably species-specific and independent of initial acclimation temperature. Each fish except largemouth bass was held at temperatures between 20 and 23 C before tests; yet, turnaround temperatures varied greatly among species. Acclimation probably increased rapidly during the 2 days preceding data collection. Within a few hours after we relinquished control of maximum tank temperature, most fish raised their environmental temperatures to the level maintained for the duration of the experiment. Investigations by Loeb and Wasteneys (1912), Sumner and Doudoroff (1938), Doudoroff (1942), Brett (1944, 1946), and Allanson and Noble (1964) suggested that our specimens should have been completely acclimated to their new thermal regimes within 1–3 days. So, after access to temperatures up to 30 C for 1 day and 40 C for an additional day, thermoregulatory behavior was presumably dictated by self-imposed acclimation levels which remained constant during the succeeding 3-day trial. There was no indication of consistent drift in thermoregulation toward either higher or lower temperatures during the trials.

Thermoregulatory performances of our fish were generally consistent with available information on their final temperature preferenda.[3] Published data are available for two of the six species; carp and yellow perch have final preferenda of 32.0 C (Pitt, Garside, and Hepburn 1956) and 24.2 C (Ferguson 1958), respectively. Ferguson (1958) cited unpublished manuscript values of 32.3 C for bluegill and 30–32 C for largemouth bass. All four species have final temperature preferenda somewhat nearer the upper than lower turnaround temperatures we recorded. Such asymmetry of turnaround temperatures relative to the final preferendum was not unexpected, because fishes typically prefer temperatures much nearer the upper than lower lethal levels (see data compiled by Fry 1964).

Effect of Food Availability on Behavioral Thermoregulation

When availability of food was independent of temperature, Lake Monona fishes of six species kept themselves within narrow intervals of environmental temperature. Further experiments with two of the species, bluegill and yellow perch, explored the extent to which behavioral thermoregulation might be altered by temperature-dependence of food availability.

Experimental procedures.—The 10 test tanks were modified so that fish gained access to food by spending time in one half of a tank but not in the other. Each tank was equipped with an automatic pellet feeder described by Neill and Byles (1972). The feeders dispensed food into one half (food side) of each tank about 25 cm from the tunnel mouth. Each 3-mm-long × 3-mm-diameter pellet fell into a small funnel, the tip of which was 3 cm beneath the surface of the water. When the pellet was wetted sufficiently to sink, it passed through the funnel tip and, unless intercepted by the fish, fell into a second small funnel. The latter funnel formed a throat into a 0.2-liter glass jar on the floor of the tank. Each pellet was available to the fish for about 2 sec while it sank through 15 cm of water between the funnels. Pellets not intercepted accumulated in the glass jar.

Each feeder was activated only while the fish was in the food side of its tank between 0700 and 1830 CST. A timer triggered a switch to supply power to all feeders potentially between 0700 and 1830. However, each feeder was energized during this 11.5-hr interval only while the fish was in the food side of the tank, the monitoring system only then closing the contacts of a relay to complete the circuit to the feeder motor. One pellet was dispensed for every 5 min the fish accumulated in the food side of its tank during the feeding period.

Three experiments were performed. In each experiment, temperature in the right side of each tank was the midpoint (Tp) of the preferred range determined from thermoregulatory tests described above. The left side of each tank was also maintained at Tp for a training period of 4 days; thereafter, the left side was either cooler or warmer than the right side.

In the first experiment, fish were offered food at temperatures above or below Tp (food side = varied-temperature side). One fish acclimated to Tp was put into each test tank, both sides of which were maintained by contact thermometer at Tp for 4 days. During this period, the fish received only food dispensed by the feeder into the left side of the tank. After the last day of the training period, between 1830 and 2000, temperature of the left side was increased 2 C in five tanks and decreased 2 C in the other five tanks. The right side of all tanks remained at Tp. Thereafter, left-side temperature was progressively increased or decreased 2 C between 1830 and 2000 on each successive day.

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[3] The final temperature preferendum (Fry 1947) is the temperature about which fish living in a temperature gradient will ultimately congregate, regardless of their previous thermal experience. Fry and others (see Fry 1964) have considered the final preferendum to be species-specific.

The second experiment repeated the first, except that the feeders dispensed food into the right side of each tank (food side = preferred-temperature side). Thus, food was available at Tp between 0700 and 1830 each day but never at temperatures above or below Tp.

A final experiment allowed fish to choose on several consecutive days between Tp without food and a single temperature above Tp with food; the object of this experiment was to determine if the fraction of time fish spent in the food side might change after the first day at a varied temperature. One fish was put into each of five test tanks, both sides at Tp, with food dispensed on the left side (food side = varied-temperature side). At the end of the training period, temperature of the left side was increased to Tp + 4 C (bluegill) or Tp + 6 C (yellow perch). This regime was then maintained 6 days with no further changes in temperature.

Bluegill (63–93 mm long) and yellow perch (105–129 mm long) were used in these experiments because of their divergent preferred range midpoints—30 and 23 C, respectively. The same specimens served in all three experiments, except that (1) the five bluegill that had experienced temperatures above Tp in the first experiment were replaced, and (2) three yellow perch that died during the first experiment were replaced. During the 16 to 18 days between experiments, the fish lived in holding tanks at Tp. Fish were individually marked with fin clips after the first experiment to ensure that each specimen encountered the same sequence of thermal environments during the second experiment as during the first. Only those specimens that had not been exposed to temperatures exceeding Tp were used in the final experiment; this was accomplished by using fish that had, during the first and second experiments, been in test tanks whose left-side temperatures were decreased.

Experiment 1. Food available at nonpreferred temperatures.—When both sides of all tanks were at temperature Tp on the final day of training, the median bluegill and yellow perch spent about 73% and 43%, respectively, of the feeding period in the side whose temperature was to be varied (Fig. 18). Then, as temperature diverged from Tp, both species progressively spent less time in the side with varied temperature. Median time spent by bluegill in the side with varied temperature dropped to 50% of the initial level at about 26 and 33 C and to 5% at about 20 and 35 C (by interpolation, Fig. 18a). Thus, the rate of decrease for bluegill was somewhat steeper as temperature increased than as it decreased. For yellow perch, time in the side with varied temperature was more symmetric about Tp and decreased less abruptly than in the case of bluegill. At about 19 and 29 C, 50% reduction occurred; at about 14 and 33 C, 95% reduction occurred (by interpolation, Fig. 18b). Data were more variable among yellow perch than among bluegill.

Most bluegill and yellow perch reduced time spent at the varied temperatures by reducing both the frequency and duration of forays into the varied-temperature side of the tanks (Neill 1971). The number of forays per feeding period was highly variable among individuals within each species. Among yellow perch, inter-individual variation in number of forays tended to increase as temperature decreased or increased from Tp. But among bluegill, variation in the number of forays decreased at temperatures above Tp. Bluegill decreased duration of forays more abruptly at high temperatures than at low temperatures. In the 8 C interval, 30 to 22 C, forays briefer than 0.5 min increased from 8% to 50% of the total number, but in the 8 C interval above Tp, 30 to 38 C, forays less than 0.5 min long increased from 7% to 95% of the total. Yellow perch may have actually increased foray duration at moderate departures from Tp (–2,

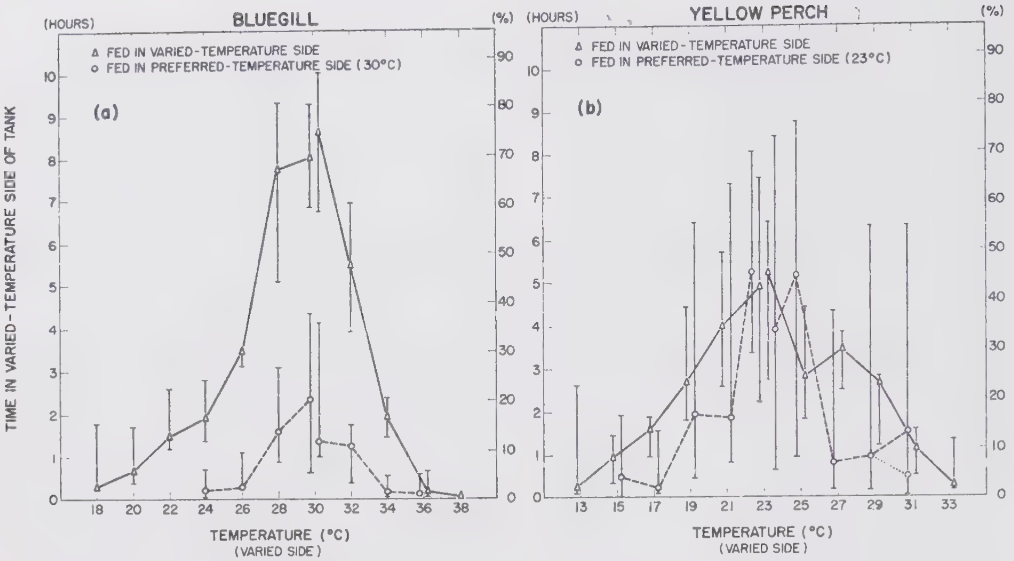

FIGURE 18.—Time spent in the varied-temperature side of tanks by bluegill (a) and yellow perch (b) fed in the side with varied temperature or in the side with the preferred temperature, Tp. Medians are given by point symbols; vertical lines about medians indicate interquartile ranges for samples of three to five fish.

+6 C), but at more extreme temperatures they made increasing proportions of very brief forays. The few yellow perch that increased the number of forays at extreme temperatures (causing increased inter-individual variation in number of forays) did so by making forays of short duration, i.e., less than 0.5 min.

Three yellow perch died during the experiment; all were in tanks with increasing temperature in the varied side. One jumped out of the 23 C side of its tank when the varied-temperature side was 31 C. The other two were found dead in the varied-temperature side of their tanks; tank temperatures were 35–23 C in each case. Both fish last entered the 35 C side during darkness (2021 and 2235 hr). They presumably died because of overexposure to 35 C, a temperature above the upper lethal limit for yellow perch (Fry 1964).

Experiment 2. Food available at the preferred temperature.—When both sides of each tank were at temperature Tp, the median bluegill and yellow perch spent about 16% and 40%, respectively, of the feeding period in the side whose temperature was to be varied (Fig. 18). If allocation of time under initial temperature conditions in this experiment was the same as in the first, the median bluegill spent 73% of the feeding period in the side with food and 16% in the side without food, whereas the median yellow perch spent almost equal time in the sides with and without food—43% and 40%, respectively. The remainder, 11% for the bluegill and 17% for the yellow perch, could be attributed to time the fish spent resting in the tunnels; these percentages were consistent with tunnel time estimated from the event-chart records.

As in the first experiment, time spent by fish at the varied temperature decreased as it decreased or increased from Tp (Fig. 18). As the varied temperature diverged from Tp, time spent by bluegill in the varied side remained dramatically below that during the first experiment. Although the difference between experiments was less marked with yellow perch than with bluegill, median times of yellow perch at temperatures above and below Tp were also significantly lower during this experiment than in the first (one-tailed Wilcoxon test; $p = 0.05$).

Responses of yellow perch were generally more varied during this experiment than in the first, and medians of time in the side with varied temperature fluctuated about the trend relating time to temperature (Fig. 18b). Among yellow perch in tanks with increasing temperature was one fish that consistently spent more than 75% of its time in the warmer side. The aberrant response of this fish affected median time most on the final day of the experiment (varied side at 31 C); on that day, another fish had to be excluded from analysis because the preferred-temperature side of its tank was potentially 3 C too warm during the first 3.5 hr of the feeding period. If data from the excluded fish were considered acceptable, median time at 31 C was reduced from 13% to 4% of total time (dotted circle, Fig. 18b).

In neither species was there a substantial change during this experiment, as compared with the first, in the *rate* at which time at the varied temperature decreased as that temperature diverged from Tp (Fig. 18). However, bluegill and yellow perch did spend more time at nonpreferred temperatures when food was available only at those temperatures than when food was available only at the preferred temperatures. When fed at the preferred temperatures, bluegill and yellow perch spent less than 5% of their time at temperatures outside the ranges 26 to 34 C and 17 to 31(?) C, respectively. These ranges were greater, 18–36 C for bluegill and 13–33 C for yellow perch, when food was not available at preferred temperatures.

As in the first experiment, each species generally reduced both number and duration of forays into the varied-temperature side as its temperature diverged from Tp (Neill 1971). In this experiment, however, differences between the experimental groups under initial temperature conditions prevented further interpretation of the foray data. Those bluegill and yellow perch destined to experience decreased varied-side temperatures made fewer and longer forays than the other experimental group during the final day at Tp. Perhaps the difference between groups was due to their different histories. All fish to be exposed to decreasing temperatures had been used in the first experiments, but all the bluegill and three of five yellow perch which were to experience increasing temperatures were naive in that they had not previously encountered food in any but the preferred-temperature side of the tank, nor had they experienced a temperature differential between sides.

Initial differences in foray behavior during the second experiment did not result in substantially different distributions of total time between tank halves. Time in the side whose temperature was to be varied did not differ significantly between experimental groups under initial temperature conditions in either of the two experiments with either species (Mann-Whitney U-test; $p > 0.6$ in each case). Similar allocations of total time were possible despite differences in foray behavior, because an inverse relationship existed between foray frequency and duration. Thus, two fish under identical conditions of temperature and food distribution tended to accumulate similar amounts of time in the varied-temperature side of the tank even though one made many short forays whereas the other made fewer but longer forays.

Experiment 3. Food available for six consecutive days at a nonpreferred temperature.—Time in the side whose temperature was to be varied did not differ significantly under initial temperature conditions from that observed in the first experiment (Mann-Whitney U-test; $p > 0.8$ for each species); median percentages of time were 76% for bluegill and 41% for yellow perch (Fig. 19). On the second day after varied-side temperature was increased to 34 C for bluegill and 29 C for yellow perch, time at the varied temperature decreased to levels similar to those observed in the first experiment (Mann-Whitney U-test; $p > 0.3$ for each species). (A decrease occurred on the first day, but difficulties with temperature control made the data unreliable.) Median times of neither species changed significantly during the remainder of the experiment (Kruskal-Wallis one-way AOV; $p > 0.9$ for each species). However, variability of time allocation among yellow perch may have increased toward the end of the experiment.

Lack of change in time spent at the varied temperature during the final 5 days of the experiment suggested that all potential adjustment to temperature heterogeneity may have been effected by the second day after varied-side temperature was raised from Tp. Al-

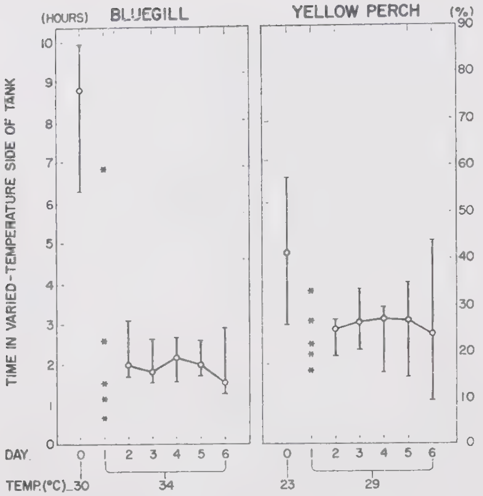

FIGURE 19.—Time spent in the varied-temperature side of tanks, at the preferred temperature (Tp) for 1 day and at a temperature higher than Tp for 5 subsequent days, by bluegill and yellow perch fed in the varied-temperature side when the other side was continuously at Tp. Sample size was three to five fish in each case; medians are indicated by circles and interquartile ranges by vertical lines. Data during the first day (day 1) at temperatures higher than Tp were considered unreliable because of temperature-control problems; the amounts of time each bluegill and yellow perch spent in the varied-temperature side of the tanks during day 1 are indicated by asterisks.

though temperature-acclimation levels of fish at the end of the experiment must have been higher than at the beginning, the data did not offer evidence for or against dependency of time at the nonpreferred temperature on acclimation level. If time allocation did depend on level of temperature acclimation, complete acclimation to 34 C in bluegill and 29 C in yellow perch may have occurred during the first day after these temperatures became available.

Discussion.—Bluegill and yellow perch responded similarly when allowed to partition their time in an environment of two parts—one with temperature Tp and the other with a temperature which increased or decreased from Tp at 2 C/day. Each species decreased the proportion of time spent at the alternative temperature as it diverged from Tp. This response occurred whether food was available at Tp or at the alternative temperature.

However, a larger proportion of time was spent at any alternative temperature when food was available only at that temperature than when food was available only at Tp. Conversely, temperatures of the alternative environment diverged farther from Tp before fish which were fed there reduced occupancy to the same proportion of time as fish fed at Tp. Alternative temperatures at which bluegill and yellow perch spent at least 5% of the feeding period spanned 8 and 14 C when food was available at Tp but 18 and 20 C when food was available at the alternative temperatures.

Although availability of food clearly biased the distribution of each species at extreme temperatures, only bluegill elected to spend a disproportionately large fraction of time in the compartment with food when both halves of the tank were at temperature Tp. The time so spent—about 70% of the feeding period—was much more than necessary to keep the stomach filled with food, even if the efficiency of pellet interception was only 50%. (Bluegill fasted for 24 hr intercepted and ate as many as 12 consecutively dispensed pellets; so, the efficiency of "hungry" fish may have been considerably greater than 50%.) A fish of median weight (10 g bluegill; 12 g yellow perch) gained potential access to its maximum daily meal[4] by spending only about 15% of the feeding period in that half of the tank with food.

Temperature did eventually limit each species' acquisition of a maximum daily meal. Bluegill did not obtain a maximum daily meal at temperatures below 24 C or above 34 C; temperatures limiting acquisition of a maximum daily meal for yellow perch were 17 C and about 30 C.

Acclimation of fishes to an increase in temperature occurs much more rapidly than acclimation to a decrease of equal magnitude (Loeb and Wasteneys 1912; Brett 1944, 1946;

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[4] Maximum daily meal, as used here, was the largest quantity of pellets a fish could consume during 11.5 hr, given that most of the food was digested at or near Tp. The maximum daily meal of both species was assumed to be about 4% of body weight. On occasions when individual fish consumed all pellets dispensed during a feeding period, the maximum amounts eaten by a bluegill and a yellow perch were 4.2% and 4.0%, respectively, of body weight.

Heath 1963). Moreover, upward acclimation over a temperature interval of given length proceeds more rapidly the higher the endpoint temperature (Brett 1946). Therefore, acclimation levels of fish that experienced increasing temperatures in these experiments may have kept pace with the 2 C/day temperature rise. In contrast, acclimation levels of fish in tanks with decreasing temperature probably remained near Tp throughout the experiments because the time spent at low temperatures was unlikely to have been sufficient for much downward acclimation.

If acclimation states were as supposed, thermal stresses governing time spent in food environments with increasing and decreasing temperature were of different types. Time spent at temperatures increasing from Tp became much reduced when those temperatures approached the ultimate incipient upper lethal limits, 35 C for bluegill and 32 C for yellow perch (Fry 1964); above these temperatures, each species spent less than 5% of time. But, both bluegill and yellow perch curtailed time to less than 5% when decreasing temperatures were still several degrees above the lower lethals for Tp-acclimated fish—about 12 C for bluegill (Hart 1952) and probably less than 4 C for yellow perch (Fry 1964). Thus, bluegill and yellow perch were practically excluded from environments with food when temperatures exceeded the ultimate upper lethals or when temperature dropped about 10 C below the acclimation temperature, Tp. In the case of increasing temperature, exclusion was apparently caused by the fishes' absolute inability to acclimate to temperatures above the lethal limits. At decreasing temperatures, however, the limits were apparently set by fishes' unwillingness to endure nonlethal stresses imposed by temperatures several degrees below the acclimation levels.

Although neither species spent much time at temperatures above the upper lethal limits, the median bluegill and yellow perch that were fed at increasing temperatures did make about 20 and 40 forays, respectively, into water 3 C above the upper lethal temperature. These fishes would have died within a few hours had passage back into the Tp environment been prevented during a foray. Perhaps the two yellow perch that died at 35 C during the first experiment were prevented from returning to 23 C by their decreased ability, in darkness, to find the tunnel.

Midpoint of the preferred temperature range, 30 C for bluegill and 23 C for yellow perch, was confirmed as a reasonably accurate estimate of the preferred temperature. Had a temperature 2 C above or below Tp been preferred over Tp, the fraction of time spent in the alternative environment at that temperature should have increased over that when both environments were at Tp. No substantial increase was observed in any of the experiments. That is, relative to an environment at Tp but without food, no combination of temperature and food was preferred over Tp with food. Also, relative to an environment at Tp with food, no temperature without food was preferred over Tp without food.

Only bluegill spent more time at some temperatures if food was offered there than at Tp without food. If 11% of each feeding period was spent in the tunnel, then the fraction of time spent in the compartment with food was not reduced to equal that spent at Tp without food (44.5%) until the temperature of the food compartment decreased to about 27 C or increased to 32 C. In this sense, the environment preferred by bluegill was shifted 3 C downward and 2 C upward from the preferred temperature by the availability of food in that environment when no food was available at the preferred temperature.

INTEGRATION AND CONCLUSIONS

Distribution of Lake Monona Fishes Relative to the Outfall Area

Lake Monona fishes were diversely distributed within the littoral zone. Some fishes regularly avoided the outfall area; these were yellow perch, mottled sculpin, subadult yellow bass, and subadult black bullhead. Others were occasionally or usually concentrated in the outfall area relative to reference areas—longnose gar, large carp, large yellow bass, young rock bass, young pumpkinseed, bluegill, and largemouth bass. Still other fishes, even though some were caught in relatively large numbers, could not be placed with conviction in either group. Among these were subadult carp, large pumpkinseed, black crappie, Iowa darter, and logperch. Thus, distributions varied not only among species but also among size classes within some species.

Distributions of fishes also differed among seasons and, within seasons, between day and night. Kinds, sizes, and numbers of fish fluctuated throughout the littoral zone. However, the abundance of most fishes in the outfall area approximated a constant ordinal relationship to their abundances in reference areas from season to season and from day to night. Although several fishes (e.g., yellow bass, bluegill, largemouth bass) tended to be more uniformly distributed at night than during afternoon, no size class of a species was significantly more abundant in one area during the afternoon but in another at night. In only two cases were there significant seasonal reversals in the ordinal relationship between areas. Small bluegill were more abundant in the reference areas during November 1968 but in the outfall area during most other seasons. Small black crappie were more abundant in the outfall area during summer 1968 but in the reference areas during summer 1969.

Fish Distribution, Temperature, and Behavioral Thermoregulation

Results of the different research phases argued jointly that the varied distributions of fishes among outfall and reference areas during summer primarily reflected different behavioral responses to temperature. The lines of evidence supporting this conclusion are listed and discussed below.

1. During summer, fishes in the outfall area were generally not uniformly distributed with respect to temperature, and different fishes tended to be most abundant within different ranges of available temperature.

Catch/effort from 50-m transects indicated that fishes were not equally abundant at all temperatures and that some fishes occurred at higher temperatures than others. More accurate description of temperatures experienced by outfall-area fishes was permitted by measurements of their body temperatures.

Measurement of body temperatures confirmed partial segregation among species with respect to temperature. During afternoon, median body temperatures of carp, pumpkinseed, bluegill, and largemouth bass were above 29 C, while those of yellow bass, rock bass, black crappie, and yellow perch were below 29 C. At night, only longnose gar and carp had median body temperatures above 29 C, whereas yellow bass, rock bass, pumpkinseed, bluegill, largemouth bass, and black crappie had median body temperatures below 29 C.

2. During late summer, young bluegill at different locations in the outfall area were acclimated to temperatures within a narrow interval of the available range.

Fish collected on five dates from four locations within the outfall area had estimated acclimation temperatures between 29.4 and 31.3 C even though water temperatures varied between 25 and 36 C at the collection sites. To have attained acclimations between 29.4 and 31.3 C, young bluegill must have spent a majority of time at or below these temperatures and almost no time above 31.5 C.

This conclusion was in substantial agreement with the distribution of body temperatures observed for slightly larger young bluegill. The highest body temperature among 31 specimens was 31.8 C; the interquartile range of body temperatures was 28.8 to 31.2 C during afternoon and 27.0 to 29.0 C at night.

3. The more abundant a species was in the outfall area relative to reference areas during summer, the higher were the temperatures in the outfall area at which representatives of that species occurred during summer.

During summer, median body temperatures of fishes in the outfall area were positively correlated (parametric $r = +0.75$) with concentration of those fishes in the outfall area relative to reference areas (Fig. 20). The correlation was highly significant ($p < 0.01$) despite probable variation introduced by measuring body temperatures in 1970 and abundances in 1968 and 1969.

Not only did fishes that were concentrated both day and night in the outfall area live there at higher temperatures than representatives of groups that were never concentrated in the outfall area (e.g., large carp vs. large rock bass), but also diel changes in the distribution of other fishes were accompanied by

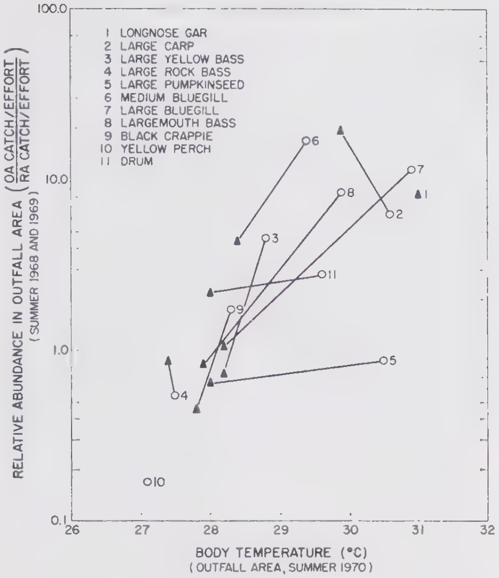

Figure 20.—Relative abundances of fishes in the outfall area during summer 1968 and 1969 compared with their median body temperatures in the outfall area during summer 1970. Data collected during afternoon and evening are indicated by open circles and filled triangles, respectively. The ordinate value of each point is the geometric mean of the values for 1968 and 1969 if data were obtained in both years (see Fig. 8).

changes in the temperatures they occupied in the outfall area (Fig. 20). Large yellow bass, medium and large bluegill, and largemouth bass were concentrated in the outfall area during afternoon but were more evenly distributed at night; within the outfall area, these fishes occurred at higher temperatures during afternoon than at night. There was little diel change in outfall-area temperatures occupied by large carp and large rock bass, whose interareal distributions remained similar from day to night.

Only large pumpkinseed during afternoon deviated markedly from the apparent relationship between body temperature and concentration in the outfall area (Fig. 20). During afternoon, large pumpkinseed occurred in water about 2.5 C warmer than was consistent with their position in the array of relative abundances. Many of these fish, including those with highest body temperatures, were caught in or near the discharge jets, to which they may have been attracted by factors other than temperature. At night, large pumpkinseed did not aggregate near the outfalls and had a median body temperature of 28 C, the same as other fishes in similar relative abundance.

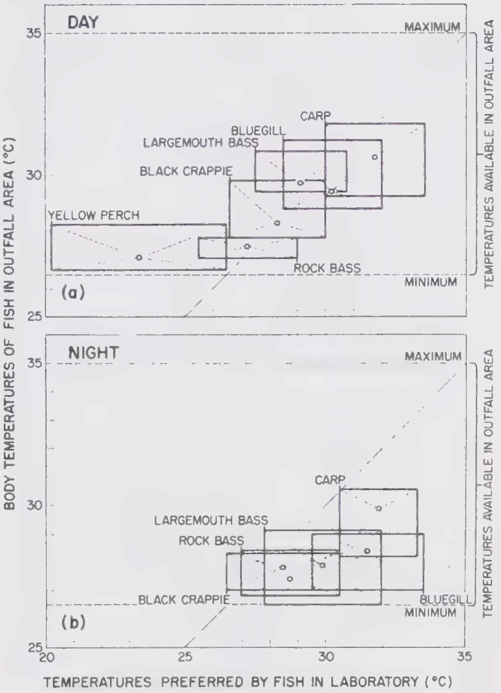

Figure 21.—Body temperatures of fishes in the outfall area in August 1970 compared with temperatures they maintained by behavioral thermoregulation in the laboratory; (a) day, (b) night. A circle indicates the median body temperature and midpoint (Tp) of the preferred range of temperature for each species. Rectangles indicate, vertically, interquartile ranges of body temperature and, horizontally, the preferred range of temperature. (The preferred range is limited by median upper and lower turnaround temperatures.)

4. Diurnal temperature distributions of six species in the outfall area during August conformed to the distributions of temperature they maintained by behavioral thermoregulation in the laboratory (Fig. 21a).

Those fishes that regulated at higher temperatures in the laboratory occurred at higher temperatures in the outfall area. Moreover, all species except yellow perch had median body temperatures in the outfall area within 1.2 C of the midpoint of the preferred range in the laboratory.

Yellow perch avoided the outfall area; they were never more than 0.15 times as abundant there as in the reference areas. The few individuals that did occur in the outfall area lived in water that was the coolest available but still warmer than the upper turnaround temperature, 26.5 C. There was little water anywhere in the littoral zone cooler than 26.5 C in August 1970.

Nocturnal temperature distributions of five species (only 2 yellow perch were caught at night) were correlated somewhat less well with thermoregulatory limits than were diurnal distributions (Fig. 21b). Some fishes in the outfall area, notably bluegill and largemouth bass, occurred at temperatures lower at night than during afternoon. While laboratory fish may have spent more time near the lower turnaround temperatures at night than during the day, turnaround temperatures remained the same from day to night and did not, therefore, reflect any downward shift in average temperatures the fish maintained.

Temperature distributions of fishes in the outfall area were assessed from specimens generally larger than those used in the thermoregulation experiment. Only the comparisons for bluegill, largemouth bass during the day, and yellow perch could be based on fish of similar size. In the other cases, few or no field data were collected from specimens as small as those convenient for use in experiments.

Considering that field and laboratory data were reasonably consistent despite variation in the sizes of fish compared, the following conclusion was suggested: The different temperature distributions of six species within the outfall area resulted from species-specific behavioral thermoregulation.

Coutant (1970), in a review of both published and unpublished literature on reactions of fishes to heated discharges, did not cite empirical evidence that fish distributions in outfall areas correspond with their thermoregulatory performances in experimental temperature gradients.

Ferguson (1958) has examined his and other data in what has been the only systematic attempt to test agreement between distributions of fishes in unheated waters and the temperatures they prefer in the laboratory. For species with lower preferenda (three salmonids, one coregonid), laboratory and field data were in substantial accordance; however, largemouth bass, smallmouth bass, and the burbot (*Lota lota*) preferred temperatures in the laboratory about 3, 6, and 10 C higher than the respective temperatures at which they occurred most frequently in lakes during midsummer. Fingerling and larger yellow perch had final preferenda of 24 and 21 C, respectively; field observations indicated that adult yellow perch live at about 21 C during summer. Largely on the basis of the data for yellow perch, Ferguson (1958) argued that fishes with higher preferenda—such as the two basses and the burbot—prefer the same temperatures in laboratory and field, but smaller individuals prefer temperatures higher than do adults; thus, the discrepancy between field and laboratory information reflected use of young fish in determination of preferenda, whereas field data were derived mainly from older fish.

Variation in preferenda of yellow perch, which Ferguson attributed to size or age, may instead have resulted from seasonal effects. Data from fingerlings were collected during summer, but older fish were tested in winter. Both the temperatures tolerated (Hoar 1955; Hoar and Robertson 1959; Neill 1967) and preferred (Sullivan and Fisher 1953; Neill 1967) by fishes may fluctuate seasonally, perhaps in correspondence with changing photoperiod. Temperature tolerances of some fishes also vary with size (Hart 1947; Hagen 1964; Neill, Strawn, and Dunn 1966; Coutant 1970), but an unequivocal effect of size, *per se*, on final temperature preferendum has not been demonstrated experimentally for any fish.

Explanations not based on a size effect may account for the discrepancies noted by Ferguson (1958) between final preferenda and fish distributions in nature. First, temperature preferenda of some fishes may exceed maximum temperatures available in unheated habitats. Second, field data reviewed by Ferguson (1958) were based partly on net catches at night, when, as present results have indicated, some fishes do occupy waters cooler than the final preferendum. Third, the final temperature preferendum may correspond more closely to the upper limit than to the lower limit of the preferred range of temperature.

In summary, major features of the littoral distributions of Lake Monona fishes during summer were consistent with the following explanation: Temperature was a major factor governing fish distribution, in that fish tended to be most abundant in that part of the habitat having temperatures within or nearest a species-specific preferred range of temperature determined in the laboratory. Disparate distributions of some conspecific fish of different size resulted from the influence of factors other than size-related differences in preferred temperature.

Fish Distribution and Nonthermal Factors: Food, Predators, Currents

Temperature has been almost universally regarded as the primary factor governing the use of outfall areas by fishes (Dryer and Benson 1957; Trembley 1961; Alabaster 1964, 1969; Alabaster and Downing 1966; Mihursky 1967; de Sylva 1969; Mount 1969; Allen, Boydstun, and Garcia 1970; Gammon 1970). In general, distributions of Lake Monona fishes in conjunction with laboratory results supported the hypothesis of thermal primacy.

However, some aspects of the distributions of Lake Monona fishes indicated the influence of factors other than temperature. Spatial segregation of young and adults of two species, carp and yellow bass, probably did not reflect size differences in preferred temperature. Adult carp were concentrated in the outfall area during summer, but young carp were not. Thermoregulatory behavior of young carp indicated that they preferred temperatures between 30 and 33.5 C—temperatures available only in the outfall area. Young yellow bass avoided the outfall area, but larger fish were relatively abundant there and were particularly concentrated near the jets. Yet, large yellow bass stayed near the bottom in water not much warmer than the reference areas where the young lived. Young rock bass were concentrated in the outfall area but lived at essentially normal littoral temperatures by avoiding locations near and between the jets. Large pumpkinseed, although not concentrated in the outfall area as a whole, lived near the outfalls during afternoon at temperatures approaching the maximum effluent temperature. Finally, greater abundance of young black crappie in the outfall area during August 1968 but in the reference areas during July–August 1969 could not be attributed to a temperature difference between years.

Although solutions are not offered for all problems referenced in the previous paragraph, some insight into their probable complexity is suggested by consideration of nonthermal aspects of the outfall environment. Nonthermal agents may have operated either independently or synergistically with each other and temperature to influence use of the outfall area by fishes.

One nonthermal effect of the power plant's operation was to increase the abundance of zooplankton in the littoral zone. Samples of zooplankton and young bluegill from the study areas during summer 1969 showed that:

1. Limnetic zooplankters, primarily *Daphnia* spp. and copepods, were 4 to 10 times more abundant in the outfall area than in reference areas, where densities of 5 to 20 animals/liter normally occurred (Brauer, Neill, and Magnuson[5]);
2. Limnetic zooplankters were very concentrated near each outfall (densities up to 350 animals/liter) and sometimes eddied at the surface in floating "mats" several animals thick and as much as a few meters in diameter (Brauer et al.[5]); and,
3. Young bluegill in reference areas fed primarily on the littoral amphipod, *Hyalella azteca* (87% of the items in sampled stomachs), but young bluegill in the outfall area ate primarily limnetic zooplankton (93% of the items in stomachs) (T. C. Byles, Laboratory of Limnology, University of Wisconsin, personal communication).

Thus, the supply of food for fish in part of the normally zooplankton-poor littoral zone was enriched by the discharge of water containing limnetic zooplankton that had been pumped through the power plant's cooling system. Young bluegill and probably other planktivorous fishes were able to exploit this food resource.

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[5] Unpublished manuscript, Garrett A. Brauer, W. H. Neill, and J. J. Magnuson: Effects of a power plant on the distribution and abundance of zooplankton near the plant's effluent outfalls. Laboratory of Limnology, University of Wisconsin, Madison, Wisconsin 53706.

The concentration of displaced zooplankton in the outfall area may have attracted such fishes as yellow bass, pumpkinseed, bluegill, and young largemouth bass. Fishes are known to aggregate in areas where planktonic food is relatively abundant (Lucas 1956; McNaught and Hasler 1961; Schaefer 1961).

Laboratory experiments with bluegill and yellow perch confirmed that fishes may be attracted to food-rich environments but suggested that attraction to food does not override behavioral thermoregulation. Provided that an environment with the preferred temperature is available, the fraction of time spent in a food-rich environment is likely to decrease abruptly as its temperature diverges from the preferred. Fishes may, however, briefly foray from an environment offering the preferred temperature, but not food, into cooler or warmer (even lethally warm) water where food is available.

Although planktonic food for fish was relatively concentrated in the outfall area, so too was the longnose gar, one of the major fish predators of Lake Monona. During summer 1968, longnose gar in the outfall area fed primarily on young bluegill (Haase 1969), which were very abundant. Low densities in the outfall area of young carp and young black bullhead may have resulted in part from predatory activities of longnose gar. Evidence from Lake Mendota suggests that young carp are more vulnerable to longnose gar than are young bluegill and other spiny-rayed fishes (Haase 1969).

The flow of water from the outfalls may have influenced the formation and maintenance of fish aggregations at the primary outfall during late winter and spring. Adult yellow bass, which dominated outfall aggregations, also concentrated during the same season in the swiftly flowing water below a navigation lock on the Yahara River between Lakes Mendota and Monona. The temperature of the river was about 8 C, while the heated effluent was 14–20 C. Strawn (1969) noted the similarity between aggregation of fishes at power plant outfalls and in reservoir spillways. Takayama et al. (1967) found that rainbow trout (*Salmo gairdneri*) gathered at an inlet discharging into the pond in which they were held. Concentration of fish occurred whether the inflow was warmer or cooler than the pond but was most marked when the influent was near acclimation temperature.

To close the discussion of nonthermal effects, we note parenthetically that low concentrations of dissolved oxygen were not observed in the outfall area. Water in the outfall area during summer 1968 was supersaturated (up to 115%) with oxygen. Other workers (Trembley 1965; Alabaster and Downing 1966) also observed little or no decrease in the oxygen content of effluent from power plants, although ". . . the spectre of loss of dissolved oxygen in power stations is continually raised by speculative articles for the layman" (Coutant 1970, p. 359).

Responses of Lake Monona Fishes to Power Plant Operation: Present Assessment and Some Unresolved Problems

Investigation of the distributional ecology of fishes in Lake Monona's littoral zone, laboratory experiments on behavioral thermoregulation of fishes, and information from the literature suggested the following major conclusions:

1. Distributions of fishes within the littoral zone of Lake Monona were markedly and differentially influenced by the discharge of heated effluent.
2. Major features of the distributions during summer resulted from fishes' different responses to elevated temperatures of the outfall area.
3. During summer, fishes avoided or concentrated in the outfall area and, within it, distributed themselves primarily in accordance with thermoregulatory behavior, whereby each individual tended to maximize its exposure to temperatures within the preferred range of the species.
4. Behavioral thermoregulation was not overridden, but in some cases may have been modified, by behavioral responses to the outfall area's peculiar nonthermal features—

abundant food, strong currents, concentrated predators.

Our work did not provide empirical evidence for or against the contention that Lake Monona fishes responded to operation of the power plant with ecological prudence, i.e., that fishes concentrated in that fraction of the habitat which was optimum for performance of their life processes. An attempt to assess one measure of young fishes' ecological success—growth rate—yielded results confounded by size-differential movements of the fish. Thus, information from other studies must constitute the basis for conjecture as to whether distribution of Lake Monona fishes reflected preference for optimum habitats.

It seems logical that fishes ought to prefer environments that are, in some sense, optimum. Experimental evidence from the literature confirms that preferred and optimum temperatures of fishes are highly correlated when other components of environment are not limiting. Among 12 physiological responses of sockeye salmon (*Oncorhynchus nerka*), only 2—food conversion efficiency and food intake—have thermal optima different from 15 C, the final temperature preferendum (Brett 1971). The final temperature preferendum, 25 C, of the guppy (*Poecilia reticulata*) corresponds to the optimum temperature for development of resistance to lethal temperatures and for maximum growth rate (Fry 1964). Young channel catfish grow fastest and convert food to flesh most efficiently at 29 C (Strawn 1969) or 30 C (Andrews and Stickney 1972); their final temperature preferendum is 29 C (Strawn 1969).

However, the optimum temperature for growth and perhaps other activities may vary with the availability of food, whereas the final temperature preferendum may not. When Brett, Shelbourn, and Shoop (1969) provided young sockeye salmon with excess food, growth was most rapid at temperatures near the final preferendum, 15 C. But when food was restricted to less than 6% of dry body weight per day, the optimum temperature for growth decreased and, at 1.5%, was only 5 C. In contrast, channel catfish fed 6%, 4%, or 2% of their weight per day grew fastest at 30 C on each ration (Andrews and Stickney 1972).

If, when food is limiting, the optimum temperature for growth does decrease and the correspondence between optimum and preferred temperatures is to be maintained, the final temperature preferendum must also decrease. Indirect evidence suggests, to the contrary, that the final temperature preferendum may not be greatly influenced by food supply. The relationship between preferred temperature and feeding level has not been systematically evaluated, but temperatures preferred by starved fishes have been reported. Opaleye (*Girella nigricans*) preferred the same temperatures whether or not they had been starved for 2 weeks (Doudoroff 1938). Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and rainbow trout—all starved 2 or 3 weeks—preferred respective temperatures 2 C higher, 2 C lower, and 4 C lower than did fed controls (Javaid and Anderson 1967). These data suggest that starved fishes prefer temperatures only slightly lower or even higher than those preferred by well-fed fish.

Both planktivorous and piscivorous fishes of Lake Monona had access to abundant food in the outfall area. Thus, fishes that during summer lived at preferred temperatures in the outfall area also encountered conditions that were presumably optimum for growth.

But if food had been deficient in the outfall area, we believe that distributional responses of fishes would have been little different from those we observed. Both temperature preferences of starved fishes (Doudoroff 1938; Javaid and Anderson 1967) and the behavior of bluegill and yellow perch offered food at extreme temperatures suggest that fishes tend to prefer certain species-specific temperatures regardless of whether or not food is available at those temperatures. Thus, a food-deficient outfall area might be expected to attract fishes that prefer high temperatures even though it would offer poorer conditions for their maintenance and growth than would be available in unheated parts of the habitat.

Whether significant advantages or disadvantages accrue to individual fish in outfall areas depends not only on "quality" of the outfall environment but also on the amount of time the fish lives there.

Although fish distributions in Lake Monona were treated as if static, dynamic features were recognized. The study areas certainly did not consist of closed systems, each with its own resident populations of fish. Rather, at any instant the assemblage of fishes in a part of the littoral zone consisted of individuals that had been there for different periods of time. That a very small fraction of marked fishes was recaptured suggested that larger fish resided in the study areas no longer than several days before they were replaced by new immigrants. Many larger fishes (adult bluegill, yellow bass) must have stayed in the littoral zone no more than 12 hr consecutively, because the individuals present in the study areas were obviously fewer during the day than at night. Presumably, smaller fishes moved about less than larger ones. However, diel changes in length-frequency distributions suggested that even small bluegill made onshore-offshore movements.

Further evaluation of the power plant's impact on fishes must await answers to the following questions pertaining to dynamic aspects of fish distribution:

1. How do fishes arrive in the outfall area?
2. How long do individual fish stay in the outfall area?
3. What factors cause fish to leave the outfall area?
4. Once a given fish has left the outfall area, is it likely to return and, if so, how soon?

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7430

Thermal Inertia versus Thermoregulation in "Warm" Turtles and Tunas

The recent report by Frair *et al.* (*1*) convinces us that large leatherback turtles (*Dermochelys coriacea*), like large pelagic fishes (*2*), can maintain body temperatures several degrees warmer than the environment. However, after cooling one turtle to determine whether the excess body temperature of another could be attributed to experimental manipulation, Frair *et al.* incorrectly computed the coefficient of temperature change, *k*. While Frair *et al.* reached a conclusion that seems substantially correct, their *k* is thermodynamically inconsistent for animals that maintain body temperatures appreciably higher than ambient temperature. Our comment is also directed to reconsideration of presumptive evidence by Carey and colleagues (*2–4*) for thermoregulation in bluefin tuna (*Thunnus thynnus*).

An object that produces no heat changes temperature at a rate proportional to the difference between its temperature (T_b) and that (T_a) of its environment:

$$dT_b/dt = k(T_a - T_b)$$

The term $T_a - T_b$ may be thought of as the driving gradient of temperature. When T_a and T_b are measured in degrees Celsius and t in minutes, the units of k are degrees Celsius per minute per degree of driving gradient.

For animals that are typically warmer than their environment, the driving gradient of temperature can be redefined to maintain logical consistency in the estimation of k (*5*). If a turtle or fish maintains a body temperature 1°C warmer than the water in which it lives, it will not cool at all unless put into water at least 1°C cooler than its body temperature. The body temperature that would ultimately obtain at any given water temperature may be called the equilibrium body temperature (T_e) for that water temperature. The difference, $T_x = T_e - T_a$, between equilibrium body temperature and environmental temperature has been termed the excess body temperature by Stevens and Fry (*6*). If heat production and heat transfer remain constant, the animal will cool or warm only if the environmental temperature falls or rises so that body temperature is no longer at the equilibrium temperature. Moreover, the rate at which the animal cools or warms will be proportional, not to $(T_a - T_b)$, but to $(T_e - T_b)$:

$$dT_b/dt = k(T_e - T_b)$$

If the animal physiologically regulates body temperature, T_x is not constant with respect to T_a, and the problem of evaluating k becomes more difficult. Either k, heat production, or both k and heat production may change as a function of T_a.

To return to leatherneck turtles, Frair *et al.* (*1*) measured the cooling rate of a 134-kg animal in Florida to establish that the 18°C excess body temperature they had measured from a 417-kg turtle in Nova Scotia was not attributable to warming or cooling during experimental manipulation. The Nova Scotian turtle had a body temperature of 25.5°C after it had been held in seawater at 7.5°C for 24 hours and then kept moist in air at 17° to 26°C for an additional hour. The Florida turtle was held at ambient temperature (?) for 6 days after capture, then cooled in a bath that decreased from 27° to 1°C in about 5 hours. The animal began the cooling experiment with a body temperature of 32°C and was still cooling at 22°C when the bath reached 1°C. The slow rate at which the Florida turtle cooled led Frair *et al.* to conclude that the large excess temperature of the Nova Scotian turtle "must have been due largely to the turtle's having been able to maintain its temperature in the cold water."

The leatherback turtle cooled by Frair *et al.* (*1*) certainly maintained an excess body temperature greater than 0°C and may actually have regulated body temperature. If one assumes that the turtle was at thermal equilibrium when the experiment started and that T_x remained constant at about 5°C throughout the experiment, then the turtle was cooling about 0.035°C per minute with a driving gradient of 16°C at the end of the experiment. Thus, k was about 0.0022°C min^{-1} $°\text{C}^{-1}$—not 0.0015°C min^{-1} $°\text{C}^{-1}$ as concluded by Frair *et al.* If, on the other hand, this turtle regulated temperature to maintain a potential excess body temperature of 18°C at an ambient of 7.5°C (like the turtle from Nova Scotia), then k was about 0.009°C min^{-1} $°\text{C}^{-1}$ when the bath was at 7.5°C (*7*). Since the two turtles were of different size and had different thermal histories, true k of the Florida turtle was probably nearer 0.002 than 0.009°C min^{-1} $°\text{C}^{-1}$.

Frair *et al.* (*1*) were right to recognize that the slow rate at which a large animal exchanges heat with its environment must be considered in any evaluation of that animal's potential for physiological thermoregulation. Among fishes, such consideration is especially appropriate for tunas (Scombridae), which have countercurrent heat ex-

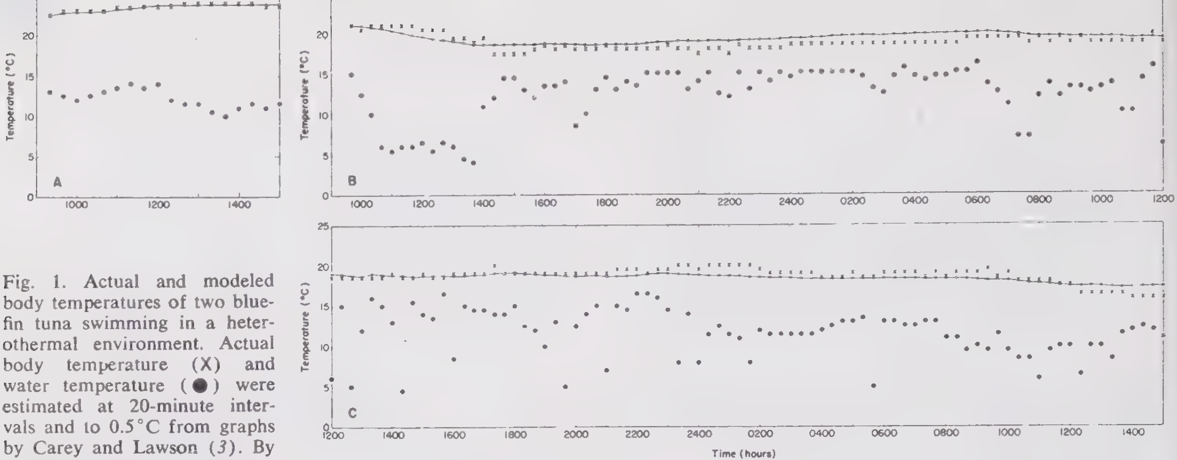

Fig. 1. Actual and modeled body temperatures of two bluefin tuna swimming in a heterothermal environment. Actual body temperature (X) and water temperature (●) were estimated at 20-minute intervals and to 0.5°C from graphs by Carey and Lawson (*3*). By exponentially filtering the water temperature series to which a constant temperature had been added, modeled body temperatures (-o-o-) were generated under the hypothesis that each fish had a constant coefficient of heat exchange and produced heat at a constant rate, that is, did not physiologically regulate body temperature. Lack of substantial physiological thermoregulation is suggested by how closely the model, optimized with reasonable values of the parameters, could be made to fit the data. (A) Muscle temperature, bluefin tuna No. 8. (B and C) Stomach temperature, bluefin tuna No. 14.

changers in their circulatory systems (*2*) and therefore might be expected to have k's approaching those of air-breathing aquatic animals and considerably smaller than the k's of typical fishes.

Large bluefin tuna have smaller excess body temperatures when caught in warm waters than when they are taken in cold water (*8*). Thus, bluefin tuna would appear to be capable of considerable physiological thermoregulation, at least when exposure to a given environmental temperature persists for the days or weeks necessary for acclimatory adjustments. On the basis of telemetry experiments, Carey and his associates (*2–4*) have carried the case for physiological thermoregulation in the bluefin further, suggesting that large bluefin subjected to rapid temperature fluctuations are capable of rapid physiological thermoregulation in the same sense as mammals. We believe the thermoregulation evident in these telemetry data was more physical than physiological—that is, that the observed responses of body temperature to changes in water temperature can be largely accounted for by a hypothesis of constant but small k coupled with constant heat production to produce a constant T_x.

To test our contention, we analyzed body temperature responses of two bluefin tuna tracked by ultrasonic telemetry through water of varying temperature. These 250-kg fish, Nos. 8 and 14, yielded what Carey and Lawson (*3*) considered the best evidence of physiological regulation of muscle and stomach temperature, respectively, among 14 bluefin tuna they monitored.

For each of the two fish, we first estimated, at 20-minute intervals and to 0.5°C, body and water temperatures from the graph of Carey and Lawson (*3*). Then, an assumed excess temperature was added to each water temperature and the resulting series of supposed equilibrium body temperatures was smoothed with an exponential filter (*9*) of the form ke^{kt} $(t \leq 0)$, where k was the coefficient of temperature change (assumed to be the same for cooling and warming) and t was time in minutes. The only actual fish temperature entering into the model was the first in the series, 22.5°C at 0920 hours for bluefin No. 8 and 21.0°C at 0940 (first day) for bluefin No. 14.

If the hypothesis of no physiological thermoregulation were plausible, some combination of constant k and constant T_x should exist to yield a smoothed series closely approximating the actual series of body temperature. For each fish, we tried several values of k and T_x; the combination we judged optimum was that which minimized the sum of squared residual errors and gave the smallest maximum residual error. Optimal k and T_x were 0.0020°C min^{-1} °C^{-1} and 13°C for bluefin No. 8 and 0.0014°C min^{-1} °C^{-1} and 6°C for bluefin No. 14. Comparison of actual and modeled body temperatures suggests that the thermal responses of these fish were generally consistent with the hypothesis of no physiological thermoregulation; maximum residual errors were only 0.3°C for bluefin No. 8 and 1.4°C for bluefin No. 14 (Fig. 1).

Moreover, the values of k and T_x giving best fit are, on independent grounds, quite reasonable. A k near 0.001 to 0.002°C min^{-1} °C^{-1} would be predicted for a 250-kg tuna by extrapolation of data summarized by Stevens and Fry (*10*) for smaller aquatic vertebrates, in conjunction with the value for the leatherback turtle cooled by Frair *et al.* (*1*). An excess muscle temperature of 13°C lies within the range expected for bluefin tuna living in water with surface temperatures between 10° and 15°C (*8*); excess stomach temperatures of bluefin range from 0°C to that of the warmest muscle (*2*).

Although our model adequately describes the major features of the bluefin data and is reasonable in its parameters, it does not eliminate the possibility that bluefin tuna can, in fact, rapidly regulate body temperature. To resolve this issue will require at least (i) careful, long-term monitoring of body temperature and activity of bluefin in heterothermal environments, together with rigorous analysis of results; and (ii) critical examination of circulatory physiology, including heat transfer and blood flow patterns, in restrained bluefin exposed to thermal stimuli.

Whether or not bluefin tuna and leatherback turtles can regulate body temperature by physiological means, their thermal inertia makes possible a kind of physical thermoregulation. Heat generated from metabolism is retained to produce advantageous (*3*) excess body temperatures, and the tissues are effectively protected from fluctuations of environmental temperature lasting even several hours. Such animals should enjoy a distinct ecological advantage over those that must rely solely on behavioral thermoregulation to maintain their tissues at the thermal optimum.

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$$dT_b/dt = k(T_a - T_b)$$

were adjusted for metabolic heat production estimated independently from oxygen consumption data.
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7. Assuming T_e was 25.5°C when T_a was 7.5°C,

$$k = \frac{dT_b/dt}{T_e - T_b} \simeq \frac{\Delta T_b/\Delta t}{T_e - T_b} \simeq \frac{-0.022\text{°C min}^{-1}}{(25.5 - 28)\text{°C}} \simeq 0.009\text{°C min}^{-1}\ \text{°C}^{-1}$$

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11. We thank F. E. J. Fry for his comments on a preliminary draft of the manuscript.

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After reading Neill and Stevens' comment, I came away with the impression that the thermoregulation we observed in bluefin tuna is in some way invalid and am concerned that it may be dismissed as an artifact of poor data analysis. I would like to point out to other readers who may have gained a similar impression that Neill and Stevens do not dispute the fact of thermoregulation, but have interested themselves in the importance of thermal buffering by the heat exchange system in achieving a stable temperature. They analyzed our experiments with bluefin No. 8 and bluefin No. 14 (*1*) and show that the observed thermoregulation could be achieved through a low coefficient of temperature change. However, this does not apply to the experiment with bluefin No. 13 (*1*). Here the stomach temperature of a 270-kg bluefin tuna increased by 7°C over a 20-hour period while the fish remained in water of constant temperature. There is more involved in the ability of the fish to control its temperature than a *k* value similar to that of a Thermos bottle.

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Evidently Neill and Stevens agree both that leatherback turtles can maintain body temperatures well above that of the environment and that the cooling rates (*k* values) for the larger turtles are in the order of 0.0015°C min^{-1} °C^{-1}. The only point of difference is that they suggest that a *k* value of 0.002 would have been appropriate, whereas Frair, Ackman, and Mrosovsky (*1*) used a figure of 0.0015. There seems little point in arguing about the exact *k* value on the basis of the meager data available. Whether a *k* of 0.002 or 0.0015 was appropriate makes little difference to the overall conclusions.

We agree with Neill and Stevens that, in principle, *k* values are better calculated on the basis of the equilibrium rather than the ambient temperature. However, in the present case, making this point is unhelpful because one does not know what the equilibrium temperature was. Moreover, Neill and Stevens have assumed that the excess body temperature is 5°C and that it would be the same at different ambient temperatures. Both these assumptions are unlikely. In using the 5°C difference they ignore data on temperature of leatherbacks in tropical waters (*2*). In suggesting that excess body temperatures are constant at different ambient temperatures, they ignore observations of increased activity of marine turtles in cooler water (*3*).

It would be desirable to learn more about the equilibrium temperatures of leatherbacks and also about the functioning of their recently discovered countercurrent system (*4*). Unfortunately there is little chance of someone with a suitable thermometer in hand encountering a leatherback in northern waters, or of a specimen in good condition being caught near adequate experimental facilities. We hope that if this should occur, someone will communicate with us so that arrangements can be made for obtaining fuller information on this warm-bodied turtle.

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15 October 1973

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A REPORT FROM THE NATIONAL MARINE FISHERIES SERVICE, SOUTHWEST FISHERIES CENTER, HONOLULU LABORATORY

Japan Tuna Research Conference
Shimizu, Japan
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By Tamio Otsu[1]

In the last 6 months, we have had to reorganize and realign our research programs in order to place major emphasis on high priority tasks. It has been decided that the Honolulu Laboratory's major thrust should be in the assessment and development of the skipjack tuna (*Katsuwonus pelamis*) resources. There is general agreement that the skipjack tuna resource is large and relatively underutilized. From the point of view of the American tuna industry, it is important to develop skipjack tuna fisheries in order to keep the industry viable, particularly the purse seiner segment of the industry. The tuna processors in the United States need new sources of raw materials, and they would like to see American interests develop the skipjack tuna fisheries. The Governments of Hawaii, American Samoa, Guam, and the Trust Territory of the Pacific Islands have raised a unified voice calling for skipjack tuna fishery development in their respective areas in order to expand their economic base. Thus, there is great interest in the U.S. very similar to Japan's current "skipjack boom."

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One of the major constraints today to the increased harvest of skipjack tuna by American interests in the central and western Pacific is the problem of live-bait supply. Although areas such as American Samoa, the Trust Territory, Guam and Hawaii all hold potential for greatly increased harvest of skipjack tuna, they are uniformly hampered by the problem of inadequate live-bait resources. The Hawaiian fishery for skipjack tuna experiences considerable fluctuations in landings from year to year. One of the reasons for the fluctuation is the shortage of live bait. The seasonal availability of the Hawaiian anchovy, nehu (Stolephorus purpureus), varies greatly, but in general the supply is insufficient to allow maximum fishing effort by the existing fleet of vessels. The problem is particularly serious during the peak skipjack tuna season, from around May to September, when many of the boats spend considerable time catching bait needed to fish skipjack tuna by the pole-and-line method. Obviously, if the boats could fish skipjack tuna instead of spending so much time in catching bait, the landings of the Hawaiian fishery would increase proportionately.

A slightly different situation applies to American Samoa and Guam. In these places, suitable baitfish are virtually nonexistent. Any fishery development would have to rely on a method of fishing that entirely foregoes the use of baitfish (e.g. purse seining) or baitfish would have to be made available (e.g. aquaculture of baitfish for pole-and-line fishing). The prewar experiences of the Japanese have indicated that bait supply was the principal factor limiting catches in the former Japanese Mandated Islands (present Trust Territory).

Purse seining may be the answer to what appears to be a universal problem of bait supply. However, experiences to date suggest that the highly developed U.S. purse seine technology needs considerable modifications before this method can work successfully in tropical waters of the central and western Pacific. Indications are, particularly from Japanese purse seine experiments, that purse seining can be made to work by modifications of the gear and by the development of new seining techniques in response to environmental conditions (clearer water, deeper thermocline) and fish behavior (smaller skipjack tuna schools, faster moving schools, etc.) in these tropical waters which are considerably different from the eastern tropical Pacific.

Both purse seining and pole-and-line fishing methods should be developed further if we are to fully realize the potential harvest of the skipjack tuna resource in the central and western Pacific Ocean. Our Laboratory, because of funding limitations, will probably not be able to carry out any extensive purse seine experiments. We feel that the U.S. tuna industry will soon begin carrying out these experiments, and we will then be providing them with whatever support possible. On the other hand, we hope to begin immediately by concentrating our efforts in the baitfish problem.

There are several possible solutions to the baitfish problem. These are 1) aquaculture of baitfish, 2) development of artificial bait, and 3) transportation of baitfish from areas of plenty to areas where they are unavailable or in short supply.

In Hawaii, some preliminary studies have shown that culturing of baitfish is not one of the better alternatives. The high cost of baitfish culture due in large part to the high cost of land acquisition is a major factor in this finding. Nevertheless, a more detailed study of the problem is needed before this alternative can be ruled out as a possible solution to Hawaii's baitfish problem. Artificial bait of various kinds has been tested in Hawaii, but results have not been too promising. The approach that seems to be most feasible at this time is to transport baitfish from California to Hawaii to supplement Hawaii's natural bait supply. If the northern anchovy (Engraulis mordax) from California can be moved to Hawaii on a regular basis in a cost-effective manner, this will permit the present fishing vessels to devote more time to fishing skipjack tuna, and enable them to increase their landings proportionately. Furthermore, the availability of bait would remove one of the major constraints to new investments in the fishery and there is every possibility that additional vessels would join the Hawaiian skipjack tuna fleet. The success of this approach requires: 1) a suitable vehicle with an effective life-support system that will permit transport of baitfish to Hawaii with little mortality, 2) a reliable bait supplier in California, 3) a reliable schedule of baitfish transport, and 4) acceptability of the baitfish by the fishermen for skipjack tuna fishing. The latter requires that the baitfish be effective in producing skipjack tuna, and that the fishermen be willing to pay for them in an amount that would make the transport program a self-paying venture. This type of action program with a good chance of immediate payoff to the Hawaiian fishing industry, and with application to other areas, is receiving our immediate attention.

We have discussed this program with members of the Hawaiian tuna industry and with various researchers, and have received enthusiastic response. The industry members have assured us that they will purchase the anchovy and, if the bait-transport system is proven cost-effective, that they will take over the full-scale system under private enterprise. Of course, we have a long way to go before a full-scale system is realized.

As a means of transporting bait from California to Hawaii, we examined several possible alternatives. For example, we considered using California albacore fishing vessels to transport the baitfish in their bait tanks. We know that anchovy can be carried in bait tanks with little mortality from previous experiences with our research vessels. However, we found that these fishing vessels cannot be depended upon to carry our bait regularly, since they would prefer to go fishing for albacore during the peak seasons. They would only agree to transport bait during their off-seasons, and this, of course, would not satisfy the requirements of the Hawaiian fishing industry.

We have also considered several other alternatives such as using a barge to carry large amounts of bait across the ocean. The costs were prohibitive. Of the several possible alternatives, we decided that the method that seems most economically feasible, and one that can be reliably scheduled, employs a large tank that can be transported over the oceans by a commercial freighter. There is a freighter running between California and Hawaii that carries roll on/roll off cargo. Anything on wheels can be rolled on in California and be transported to Hawaii in 4 days. The ship makes a round trip to Hawaii every 10 days.

The next step was to locate a bait-transporting tank on wheels. We found a surplus U.S. Navy aircraft refueling tank that seems to meet the requirements. The tank is on a trailer and is towed by a tractor. We acquired both the tank-trailer and the tractor, and began modifying it for use as a bait transport. The tank has a 5,000-gallon capacity. Large hatch covers were welded over each of the three compartments in the tank for easy access. We then proceeded to build a life-support system consisting of a gasoline pump to circulate water in the tank, a filter, an aerator, etc. The tank is made to operate with both a closed, recirculating system ashore and an open system while in transit on the freighter. The water supply will be furnished through the ship's system.

We began working on this tank in November, and have essentially completed the modifications including cleaning of the tank, painting of the interior, building a life-support system. The schedule calls for testing of the system in Honolulu with a load of threadfin shad (*Dorosoma petenense*) before shipping the tank to California for additional on-shore tests with northern anchovy. One of the important tests in California will be to determine the bait-carrying capacity of the tank. When everything is found ready, we will make the first trial shipment. We hope that by early next month (March 1974) the first trial shipment can be made.

Some of the problems that need to be overcome include: 1) obtaining strong bait in California, 2) providing sufficient circulation and aeration of the water to insure sufficient oxygen since oxygen consumption increases markedly with increase in water temperature, 3) developing an efficient method of removing dead bait from the tank, and 4) developing a method of transferring the bait from the tank to the fishing vessel with little mortality. All of these are difficult problems but we are hopeful of solving them one at a time.

One of the most serious problems is the matter of circulation in the tank since this tank was not originally built for carrying fish and the shape is far from optimal. There is little that can be done about this. Oxygen consumption is another serious problem. We have based our oxygen requirements on some data published in the Katsuo-Maguro Nenkan, 1971 (data attributed to the Mie Suishi) and also on some of our own experiments at the La Jolla Laboratory. At the La Jolla Laboratory we have conducted oxygen consumption tests at temperatures ranging from 16° to 28°C or roughly the temperatures encountered in the crossing from California to Hawaii. Fortunately, the temperature change is rather gradual, unlike the abrupt temperature increases experienced by Japanese vessels when heading for the southern fishing grounds.

If we can transport anchovy from California to Hawaii in sufficient quantities and on a regularly scheduled basis, this will not only permit our existing boats to spend more time fishing, but will encourage new vessels to join the fleet. Already there is considerable interest in new investments, but these are discouraged by the problem of bait supply. If bait supply is no problem, it is very likely that new boats will come into Hawaii, and that there will be a considerable expansion of the fishery.

At the present time, a group of researchers is readying the tank for a trial shipment of anchovy from California to Hawaii. Before shipping the tank to California, the life-support system will be tested in Honolulu with a load of threadfin shad. If the shad can be held in a closed recirculating system, then the tank will be sent over to Los Angeles by way of commercial freighter for another on-shore test with northern anchovy. The optimum carrying density will be determined before the first trial shipment. I hope that this experiment works well, and that we can prove this system to be cost-effective. By demonstrating to the Hawaiian tuna industry that an adequate bait supply can be moved to Hawaii in this manner, we are hopeful that the industry will take over the system for a full-scale operation.

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Optically effective area of particle ensembles in the sea

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Abstract

The optically effective area (OEA) concentration of particles was computed from measured size distributions and concentrations of particles in the upper 100 m of the Pacific Ocean off Baja California and is shown to correspond closely to direct measurements of the volume coefficient of light scattering at an angle of 20°, shown previously to be proportional to total scattering.

Plots of OEA as a function of particle diameter exhibit a maximum contribution at about 2 μm diameter at offshore stations and at 3.5 μm at nearshore stations. The roll-off at smaller particle diameters is attributed to diminished optical efficiency rather than to decreased concentrations of smaller particles.

Size distribution of particles in seawater and its effect on the optical character of the ocean have received increasing attention both as biological and as physical problem areas. A degree of confusion is apparent from previous work as to the size of particles which contribute most heavily to light scattering in the sea; I have tried to clarify this relationship by combining Coulter measurements of particle size distributions with light scattering measurements. By applying scattering theory to these measurements, I estimate the contribution of particle size fraction to the total light scattering.

The current confusion on this subject is due almost certainly to differences in methods used as well as to real variations in time and space. Burt (1955, 1958) inferred from selective attenuation characteristics a predominant effect of small particles (< 1 μm diameter) in Chesapeake Bay and in the eastern tropical Pacific. Sasaki et al. (1960, 1962) obtained similar results by fitting observed scattering functions of deep water samples to theoretically derived curves. Hinzpeter (1962) and Hishida (1966) inferred from color dispersion of scattered light that particles of 1–2 μm diameter predominate, though without regard to particle pigmentation. Also inferring particle characteristics from optical measurements, others (e.g. Joseph 1955; Hanaoka et al. 1960; Jerlov 1961; Duntley 1963) concluded that particles larger than 1–2 μm control optical characteristics.

A few investigators have worked with both optics and particle size characteristics; their conclusions also are somewhat conflicting. Jerlov (1955), Pickard and Giovando (1960), and Ochakovsky (1966) have made microscopic counts of particles in addition to optical measurements: they determined dominant optical effects of particles of, respectively, 16 μm, 7–17 μm, and < 1 μm diameter. Beardsley et al. (1970) and Carder (1970), using light scattering and electronic particle counting, concluded that the median particle diameter at eastern tropical Pacific stations was < 1 μm; size distributions were well described by a two-parameter exponential equation. Pak et al. (1971) computed scattering for a measured log-normal distribution of minerogenics, indicating that 90% of total scattering was due to particles in the diameter range 0.6–8.6 μm, in essential agreement with Tucker and his associates (e.g. Tucker et al. 1969) who found that 68% of particles that affect beam attenuation are less than 10 μm diameter, and 96% are less than 13 μm.

Working with particle size characteristics but without optical measurements, Lisitsin (1961) showed a predominance of particles with diameters around 1 μm, whereas the work of Krey and his associates (e.g. Krey 1961) indicates dominance of larger size fractions. Bader (1970), working with electronic particle counts of nearshore water samples, described hyperbolic distributions of size. Zeitzschel (1970) presented electronic counts which indicated numerical dominance of small particles, but, in terms of volume, larger particles contributed nearly as much as small ones to the total.

The methods used to date to provide independent measures of particle size unfortunately have a lower limit of resolution of about 1 μm and a falling-off of accuracy as this limit is approached. Direct evidence of the dominance of particles of this size and smaller is thus lacking. Most of those who conclude that these small particles account for most of the scattering do so on the basis that their assessment of somewhat larger size fractions fails to account for the observed optical effects. Particle sizes above those measured may also contribute to variation of scatter, although preliminary experiments (Owen 1972) show that this is not the case where my measurements were made.

There is, on the other hand, agreement based on measurement that light scattering is predominantly due to particles that are large compared with the scattered wavelength: nearly every observation in natural waters exhibits an intense forward component of scattered light and independence of wavelength over much of the visible spectrum.

Theory

From the Mie (1908) solutions for scattering of a monochromatic plane wave incident on a homogeneous, isotropic sphere, van de Hulst (1957) derived an expression relating the volume scattering coefficient s to the total particle cross section $N\pi r^2$

$$s(\lambda, r, n) = \int_0^\infty Q(\lambda, r, n)N(r)\pi r^2 dr. \quad (1)$$

The term Q is the scattering efficiency, the ratio of the light flux scattered at wavelength λ by a particle of radius r and relative index of refraction n to the flux incident on the particle. The scattering efficiency of single particles is related by the Mie theory to wavelength, particle radius, and index of refraction (Fig. 1, curve a). In the presence of a range of particle sizes, the oscillatory character of Q is smoothed (curve b—van de Hulst 1957). This damping effect was confirmed experimentally by Hodkinson (1963), who worked with polydisperse suspensions of irregularly shaped particles (curve c). He also demonstrated that particles of irregular shape scatter as would spheres of equivalent volume. Hodkinson's results are of immediate interest because they confirm theory by the use of suspensions similar to those encountered in the sea in that both have a wide range of particle sizes and shapes.

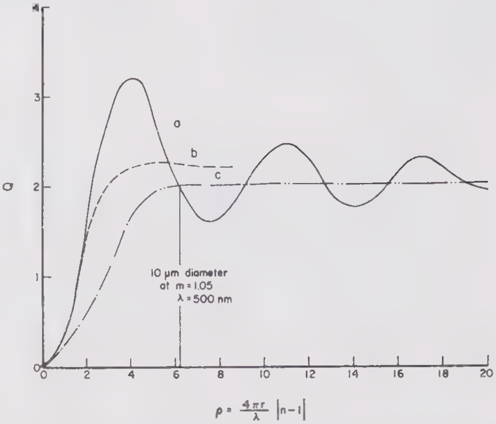

Fig. 1. Scattering efficiency Q as a function of the particle size parameter ρ. a—Function for single spherical particles; b—function for a polydisperse ensemble of spheres; c—experimental function observed for polydispersed ensembles of irregularly shaped particles.

Methods of measurement and data analysis

Measurements of particle size distribution and light scattering were made at 12 stations off the west coast of Baja California and of size distribution alone at two additional stations (Fig. 2). At stations where paired measurements were made, a submersible scattering meter was lowered slowly to 100 m to provide a continuous trace on a shipboard recorder of scatter vs. depth. Upon recovery of the scattering meter, cleansed polycarbonate sampling bottles were lowered to capture water for

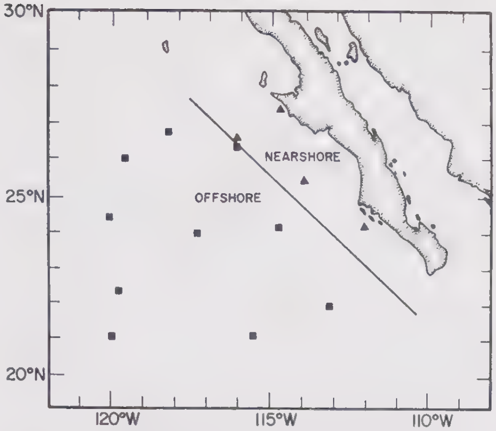

Fig. 2. Measurement locations off Baja California. Also shown is the separation of "nearshore" and "offshore" stations used (*see text*).

particle size analysis from one to four depths selected on the basis of the scatter record obtained minutes before; these were subsampled gently on recovery and particle size analyses performed within an hour. The scatter measurement was made at the single forward angle of 20°, chosen to maximize the light flux sensed by a multiplier phototube from a 0.6 cm^3 volume irradiated by a collimated light beam while still maintaining a well defined forward angle (*see* Owen 1972).

Particle size analyses were made with a Coulter counter (model B, Coulter Electronics) using general procedures given by Sheldon and Parsons (1967) for calibration and operation. Sensitivities and threshold settings were chosen to obtain particle counts in size categories that would yield numbers of particles in arithmetic and geometric progressions of particle cross-sectional areas for each sample. Numbers of particles were measured over intervals of 1.0 μm^2 from 2–16 μm^2 and over intervals of 2^n μm^2 from $n = 1$ through $n = 10$, i.e. from 2–1,000 μm^2 (1.6–36 μm equivalent diameters). A 50 μm diameter orifice was used to count particles up to 6.4 μm diameter and a 100 μm orifice thereafter. Counts made at sea were repeated when it was seen that the ship's motion caused back flushing of the sample or when clogging occurred. Counts in each size interval usually were replicated and repeated when differences exceeded roughly 5%. Methods of the particle size analysis are described elsewhere (Owen 1972).

One source of error was found by matching particle samples with values on the continuous vertical profile of scattering—vertical displacement of the pycnocline between measurements was occasionally apparent from measurement of temperature and salinity profiles obtained before and after scattering meter and sampling bottle casts and from comparison of the light scattering profile with computed water density structure. To reduce these matching errors, where they were obvious, alternate values of scattering were determined by shifting the scattering profile vertically to obtain closest consistent agreement between scattering and profiles of particle mass and carbon concentration in the pycnocline layer. A better fit could be found because the latter particle measurements were more closely spaced. These "best fit" values are shown separately and used for computation herein. Clearly, however, residual errors from this source of variation remain because not all profile pairs could be matched perfectly.

Scattering efficiency for each particle size interval analyzed in the Coulter counter was estimated graphically by finding the respective Q values from Hodkinson's (1963) experimentally determined curve (curve c, Fig. 1) which corresponds to each value of ρ. Values of ρ, in turn, were computed from the midpoint particle radius r of each size interval from the equation

$$\rho = (4\pi r/\lambda)|n-1|,$$

using 500 nm for the wavelength λ, close to the peak sensitivity of the scattering meter used, and 1.05 for the relative refractive index of the particle ensembles measured.

The value 1.05 for the refractive index was chosen as the most likely one for particle ensembles in surface waters having small sediment loads. The true value and variation of the index for surface layers are as yet only approximately known, but are converging to a value such as that used here with application of new methods (e.g. Gordon and Brown 1972; Carder et al. 1972; Zaneveld and Pak 1973). Values for individual components range widely (Jerlov 1968) but it is obvious that natural ensembles within specific areas and depths of the open sea have more nearly constant composite indices of refraction because the composition of such ensembles is not highly variable. The possibility that refractive index may be size dependent in surface layer waters cannot yet be evaluated. Differentiation of the composite refractive index into two components is desirable to the extent that the composite refractive index is size dependent. Gordon and Brown (1972) attempted to distinguish organic and inorganic fractions from their derived composite refractive index of 1.05 (for Sargasso Sea particles). They found that differences between each of their two-component models were, in fact, sensitive to whether size dependence of the refractive index was assumed, and that, in each case, organic particles dominated over inorganic. Brown and Gordon (1973), constructing two-component models, concluded that only models with organics predominating at small size ranges (<2.5 μm) and inorganics predominating at larger size ranges could account for observed scattering. Their argument would, however, be altered by using an index of refraction somewhat higher for the organic fraction than the 1.01–0.01i used.

From the values of scattering efficiency and of particle numbers measured in each size category (i), I computed the optically effective area (OEA_i) by a form of the integrand of equation 1

$$\mathrm{OEA}_i = Q_i N_i A_i,$$

where A_i is the midpoint cross-sectional area of equivalent spheres in the size category.

To make the data from all samples comparable, I summed the OEA_i values for each sample over the observed range of sizes (1.6–36 μm diameter) to obtain a total measured OEA and computed the percent contribution to the total for each size category. These percentages were then averaged over all comparable stations within each size category for a composite of percentages as a function of diameter. Variation about these mean values was too small to plot geographically in the important small size categories. Individual station plots of OEA vs. particle diameter are available from me or may be computed from the individual plots of particle size distributions given elsewhere (Owen 1972). The final step was to remove the effect due to unequal size intervals from the percentage distribution: cumulative percentages were plotted as a function of diameter, a smooth line was drawn through the points and then differentiated by graphical methods to yield the distributions shown in Figs. 3 and 4.

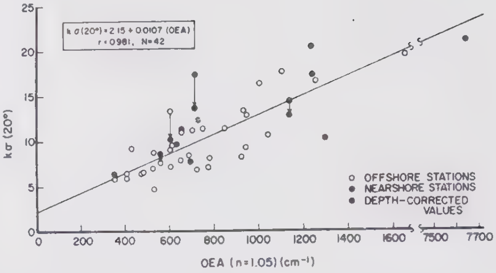

Fig. 3. Correspondence of forward light scattering at 20° off the beam axis with total measured optically effective area (OEA) from 42 paired observations. The relationship and correlation coefficient r, computed statistically, are shown in the inset. Values corrected for depth-matching error (cf. text) are shown as solid circles and are connected to the uncorrected plot.

Results

To demonstrate the correspondence of OEA computations to measured optical values, the relationship of 20° light scattering to OEA concentration of particles from 1.6–36 μm diameter, the size range indicated by Morel (1973) to contribute about 80% to scattering at this angle, is shown in Fig. 3. The correlation coefficient of 0.98,

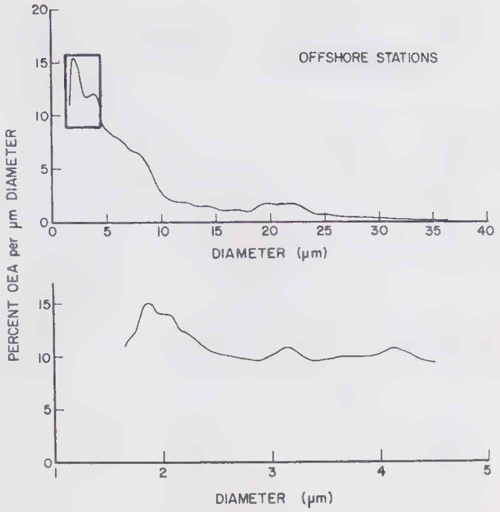

Fig. 4. Composite percent contribution to total measured optically effective area (OEA) per unit particle diameter as a function of particle diameter from 35 samples at offshore stations. Upper panel presents an independently determined subsection of the function shown in the lower panel.

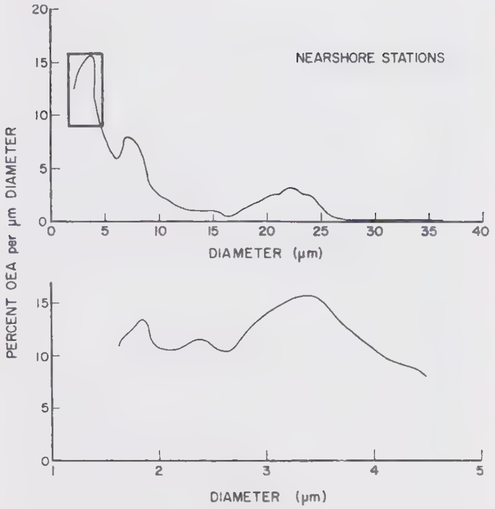

Fig. 5. Same as Fig. 4 except from 11 samples at nearshore stations.

computed using depth-corrected data pairs shown in the figure, can be considered good in view of the sources of error. These sources include variation of particle size distribution beyond the stated limits of measurement; possible variation between samples of the composite refractive index; variation of the relationship of 20° scatter to total scatter; error not already accounted for in the depth matching of discrete samples with scattering profiles. The last two sources are likely to contribute more to the residual variance than the others, although it is obviously desirable to obtain measurements of size distribution of particles below 1.6 μm and above 36 μm diameter.

The contribution by particles of given size to total OEA, determined as described above, is shown in Fig. 4 (offshore stations) and Fig. 5 (nearshore stations). This separation of offshore and nearshore stations was made on the basis of the consistent differences between particle size distributions and physical oceanographic characterstics (*see* Owen 1972). Stations were divisible by these criteria into two discrete groups, one located in an upwelling-influenced area off the west coast of Baja California and the other contiguous and seaward of the first. The difference between these areas also is apparent from the OEA percentages: contributions from particles in the vicinity of 7 μm diameter and 22 μm diameter, relatively pronounced in the nearshore group, are much attenuated offshore. Identification of these particles was not done although it is reasonable to consider them a biological expression of upwelling.

Perhaps the most significant feature of these curves is the maximum OEA contribution that occurs at about 2 μm diameter offshore and 3.5 μm diameter nearshore. This denotes that particles smaller than 2 μm make a decreasing contribution to light scattering with decreasing diameter, even though they are increasingly numerous (Carder et al. 1971; Owen 1972; Sheldon et al. 1972). This maximum and the subsequent decrease occur because the scattering efficiency of particles decreases (cf. Fig. 1) although it has not previously been demonstrated that the scattering efficiency decreases faster with decreasing particle size than the corresponding increase in particle cross-section concentration in seawater.

The curves lend support to those workers who have inferred that particles < 5 μm diameter dominate light scattering in natural waters. They do not, however, support the contention that particles with diameters less than 1 μm contribute most heavily to light scattering in the euphotic zone of waters without heavy sediment loads. A growing body of evidence (Carder et al. 1971; Owen 1972; Sheldon et al. 1972) suggests a general constancy over a wide range of particle sizes of the size distribution of particles in the upper layers of the open sea. Even though particles < 1.6 μm diameter were not measured here, the roll-off below 2–3 μm is an indication that the OEA contribution from particles < 1.6 μm continues to decrease with decreasing size.

The tendency to dominance by smaller particles in clear oceanic waters, noted by Kullenberg (1969) in comparing three widely separated areas, is confirmed here in comparing contiguous rich and poor waters. Kullenberg's finding that a predominance of particles at 3.5 μm diameter occurs in the Baltic, however, is only fortuitously close to the nearshore value shown here, because Kullenberg assumed normal distribution of particle sizes.

The quasi-stationary distribution of particle size referred to above also suggests generality of the form of the contribution to OEA from various particle sizes shown in Fig. 4. The location of the maximum contribution to OEA is sensitive to the composite refractive index of the particle ensembles. Subsequent work may show a value different from that used in the calculations presented here (1.05) or a variation of values. Refractive indices larger than 1.05 would shift the contribution maximum to smaller particle diameters: this would be expected in the deep ocean where small inorganic particles predominate. The point remains, however, that a maximum likely exists in the important upper 100 m of the sea, and that it is probably located at diameters of particles that can be measured conveniently in unpreserved whole water samples in the field.

Particles in the upper layers of the sea, as pointed out by K. Carder (personal communication), could have size-dependent refractive indices. Partly because this would affect the size of maximum contribution to light scattering, independent measurements of refractive indices are needed for natural particles, especially at the poorly understood small size fractions. Work with two-component models such as that of Brown and Gordon (1973), together with firmer estimates of refractive indices, should be helpful.

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INTRODUCTORY REMARKS

BRIAN J. ROTHSCHILD

It is a great pleasure to welcome you to the California Gray Whale Workshop. The Workshop is being held in a significant location and at a particularly appropriate time.

The location, La Jolla, is of course, quite near the area surveyed as part of the well-known California gray whale census and is also a focal region for other studies on the dynamics and life history of the California gray whale. Some of this research will be presented at this Workshop where you will hear about such diverse topics as husbandry, respiration and metabolism, cardiovascular physiology and blood studies and behavior and physiology — all related to the California gray whale.

In addition to being a region where many contemporary studies on the gray whale have been undertaken, it was also in this general area of the North American coast that Charles M. Scammon, whaler and sometime captain in the U.S. Revenue Marine, undertook his early studies of the natural history of the gray whale. His studies "The Marine Mammals of the North-Western Coast of North America," were published in 1874. Many of Captain Scammon's observations on the gray whale were made in the mid-1850's when he discovered a major nursery ground of the California gray whale in a Baja California embayment, Laguna Ojo de Liebre, now frequently called Scammon's Lagoon. Scammon was also involved in the early, intensive harvest of this species, an activity that was terminated in 1946 when the International Whaling Commission declared the gray whale a protected species.

The timing of this symposium is also appropriate. There is now an unprecedented interest in marine mammals. TV, radio, motion pictures, newspapers and magazines have all contributed to a growing public awareness and concern with these fascinating animals. Unfortunately, this deluge of publicity has resulted in a mixture of fact and fiction. The fiction has been further fed by various indiscriminate interpretations which often accompany events of high publicity value, inadequate data collection, and difficulties in interpreting the sparse marine mammal data. Further complications arise from conflicting and contradictory views of special interest groups that influence resource decisions. A case in point is, of course, the blue whale.

Because this is also a time when significant policy and conservation decisions are being made on marine mammals, it is particularly important to concentrate on the generation of factual information. The conservation of our resources is essentially a decision-making process; this process can only be effective if decision-makers are supplied with appropriate facts. Workshops such as this California Gray Whale Workshop will do much to contribute to our understanding and knowledge of marine mammals and assist in making better resource decisions which hopefully will preserve these Leviathans for the education and enjoyment of future generations.

I think Herman Melville had a premonition that all of this would come to pass; that status of marine mammal stocks would be of world concern and as a small part of this concern we would be holding our workshop. In fact he could be before you now saying, as he did in *Moby Dick:*

> "Already we are boldly launched upon the deep; but soon we shall be lost in its unshored, harborless immensities. Ere that come to pass; ere the Pequod's weedy hull rolls side by side with the barnacled hulls of the Leviathan; at the outset it is but well to attend to a matter almost indispensable to a thorough appreciative understanding of the more special leviathanic revelations and allusions of all sorts which are to follow.
>
> It is some systematized exhibition of the whale in his broad genera, that I would now fain put before you. Yet is it no easy task. The classification of the constituents of a chaos, nothing less is here essayed. Listen to what the best and latest authorities have laid down . . ."

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Fishery Potential from the Oceanic Regions

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This paper has a scope as vast as the oceanic province itself. Not only is the oceanic province extremely large, but relative to the various other regions of the ocean, very little is known about the resources that occupy its waters. Because so little is known about the oceanic province, inferences on this region tend to be based upon the more complete knowledge of the shallower coastal areas. In addition, the myriad of species and the vastness of the area require that a brief exposition such as this be treated with a rather broad brush. Thus, while my original intent was to treat the North Pacific Ocean, it appeared from the level of knowledge on oceanic resources and the degree of generality and exposition which conform to the style of these Colloquia that the discussion might better be served by a review of the fishery resources of the oceanic province in general. Rather than run through the traditional list of oceanic species or attempt to devise fixed estimators of the potential oceanic fishery production, I shall concentrate upon a few concepts which are used to determine this production, namely extrapolation from trends in present catches and food chain dynamics.

Estimation of the magnitude of resources of the oceanic province involves questions of practical as well as academic importance. Fish are an important element in world commerce, and they are likely to become more important in the future. Fish are also a particularly important commodity to the developing countries, perhaps not so much as a nutritional additive, but as a source of raw material which can be utilized to stimulate economic growth, thus contributing to international stability. This increase in the significance of fishery resources will be accompanied by (1) a reduction in the rate of catch increase for conventionally harvested species and in some instances decreases in the catch; (2) increases in national jurisdiction over fishing stocks that will reduce free access to them; (3) a rise in costs associated with conventional fishing technology; and (4) an increased demand for fishery products.

From the practical point of view we must ask how we can make the best use of our fishery resources, whether they be coastal resources or oceanic resources. There are of course many alternative paths to the development of unused resources and to the "wiser use" of those fishery resources which are already utilized. These alternative paths toward development of fishery resources exist in both developing and developed nations and in coastal waters as well as oceanic regions. The best alternative path for fishery development will depend to a large extent upon the physical capability of the various resources to produce sustained yields. This point is evidenced by noting that the present annual world catch of marine fish is about 60 million metric tons per year. If we anticipate the maximum sustainable catch to be about 80 million metric tons, our developmental strategy would be considerably different than if we anticipate the maximum sustainable catch to be 200 million metric tons. It is, therefore, important that the analysis of the maximum sustainable catch be made with great care and responsibility because appropriate development and utilization of our fishery resources are essential parts of our general resource problems.

In order to guess at the future production from the oceanic region, it is useful to attempt to extrapolate from present trends in world catches in general. These oceanic resources include the tunas, the billfishes, the squids, the flyingfish, the dolphin, and a myriad of various deepwater and surface species. The trends in catches have been reviewed by Gulland (1971). He observed a rather steady increase, at a rate of 7 percent per year, in the world catch. The world catch in 1938 was 21 x 10^6 tons, in 1956 it was about 30 million tons, and in 1970 it was nearly 70 million tons. The increase of 7 percent per annum has, of course, been compounded by declines and increases in individual fisheries as well as the institution of new fisheries and the elimination of others.

Gulland (1971) points out that in terms of new fisheries we have the following:

Peruvian anchovetta	(1955)	60,000 tons	(1961)	5 million tons
Norwegian mackerel	(1963)	20,000 tons	(1967)	870,000 tons
Thailand otter trawl.................	(1962)	78,000 tons	(1965)	337,000 tons
Southeast Atlantic hake	(1962)	100,000 tons	(1966)	410,000 tons

Off our own Pacific coast we have had some dramatic increases in catch of hake and other groundfish, and there is considerable potential increase in the catch of some fish such as the anchovy. On the other hand, we have had declines in some fisheries in the North Pacific such as the famous sardine decline, king crab in the Subarctic Pacific, and sauries off Japan. The yellowfin sole peaked at 500,000 metric tons in 1960 (estimated population 500,000 metric tons in 1964). Some fisheries have declined elsewhere, such as the herring in the Atlantic. Because of these rather short-term fluctuations it is rather dangerous to extrapolate from catch trends in individual stocks. Nevertheless we can make some interesting generalizations about the increases in catch:

1. The world catch continues to increase.
2. New fisheries must be found to maintain the increases in total catch.
3. Since relatively few individual fisheries have become extinct (possibly owing to a damping off in fishing effort as the stocks decline in density), we must be fishing an increasing number of species.
4. Fishing changes the productivity of stocks by changing mortality rates, and one can speculate that greater total yields might be obtained from many overfished stocks than from a few moderately fished stocks.

If the increase of 7 percent per year were to continue, we would hit somewhat more than 100 million tons (of conventional forms) by 1980 and about 800 million tons by the year 2000. Most authors feel that the final limit is of a magnitude closer to 100 million tons than to 800 million tons. If we can proceed, however, to several hundred million tons per year, we will almost certainly be exploiting nonconventional fisheries such as squid, larger zooplankton, and small oceanic fish. We would almost certainly need to consider harvesting significant quantities of the oceanic forms if it were possible to do so.

The Pacific Ocean has traditionally supplied somewhat less than half the total world catch, and there is no reason to doubt that it will continue to do this. For the total world catch to exceed 100 million tons and the Pacific to go beyond about 50 million tons, there will need to be considerable reliance on the nontraditional types of fish. Before these fish can be caught, it is almost certain that new technologies will have to be developed. In fact, these technologies are probably a major constraint upon the harvest of oceanic fishes. The potential catches of the various oceanic forms have been summarized by Gulland (1971) from extrapolation and other evidence (Table 1.).

It is interesting to note that the total scombrid catches, primarily the large fish, have remained stable over the last several years at about 1.5×10^6 to 1.6×10^6 tons, so large increases in these forms (with the

Table 1. Summary of potential catches from oceanic resources

Type of fish	Tons
Whales	
Large baleen (1,900 Blue Whale Units)	1,640,000
Sperm whales (25,000 animals)	500,000
Small whales	500,000
Dolphins, porpoises	?
Salmon	
North Pacific	500,000
Atlantic	15,000
Tunas	
Large tunas	
Pacific	350,000 – 450,000
Atlantic	200,000 – 250,000
Indian Ocean	100,000 – 150,000
Skipjack	
Pacific	500,000 – 800,000
Atlantic	250,000 – 300,000
Indian Ocean	160,000 – 300,000
Other small tunas	
Frigate mackerel	(1,000,000)
Bonito	(500,000)
Little tuna	?
Thynnus tonggol	?
Sharks	(500,000)
Coryphaenids	(1,000,000)
Squids	10-100 million
Myctophids, etc.	Hundreds of millions
Red crab	(1,000,000)

Note: Salmon are included here because most of their growth is accomplished in open oceans. (From: *The Fish Resources of the Ocean.* FAO, 1971, J. A. Gulland, ed. Fishing News (Books) Ltd.).

exception of the skipjack tuna) are unlikely. Also, of the important tunas of commerce, roughly 65 percent are caught in the Pacific Ocean, 10 percent in the Indian Ocean, and 25 percent in the Atlantic Ocean. Very roughly, 50 percent of the world ocean is the Pacific, 30 percent the Atlantic, and 20 percent the Indian, which suggests only on the basis of surface area that larger catches may be expected from the Indian Ocean.

If we are to have really large increases in world catch, they are likely to come from the oceanic regions. We have so little experience with the oceanic regions that there is little basis for extrapolation, and this raises the question of using an alternative procedure to guess the potential yield of fish from the oceanic region. The best known alternative procedure is to estimate the potential production of an oceanic region on the basis of primary production and the production at each successive stage in the food chain.

The classic food chain argument is extremely simple. I shall reiterate it here so that I can base my further remarks on certain of its aspects. The food chain can be viewed as a collection of factories. This is diagrammed in Figure 1. An extremely important aspect of this scheme is the number and configuration of the factories. The real "road map" could be quite complicated with such things as multiple tracks, switching yards, and tracks that pass at least once through the factory of origin before reaching the factory of destination. Furthermore, each factory has been treated essentially as a "black box," measuring only the inputs and the outputs without considering the internal working mechanism. (There are, of course, a number of papers that consider internal working mechanisms of the factories, but most of the literature on food chain estimation of production tends to be unconcerned with the details of the phenomena that occur in the "factories." Indeed, the system may, in many respects, be less sensitive to the workings of the factories than to the number of factories.)

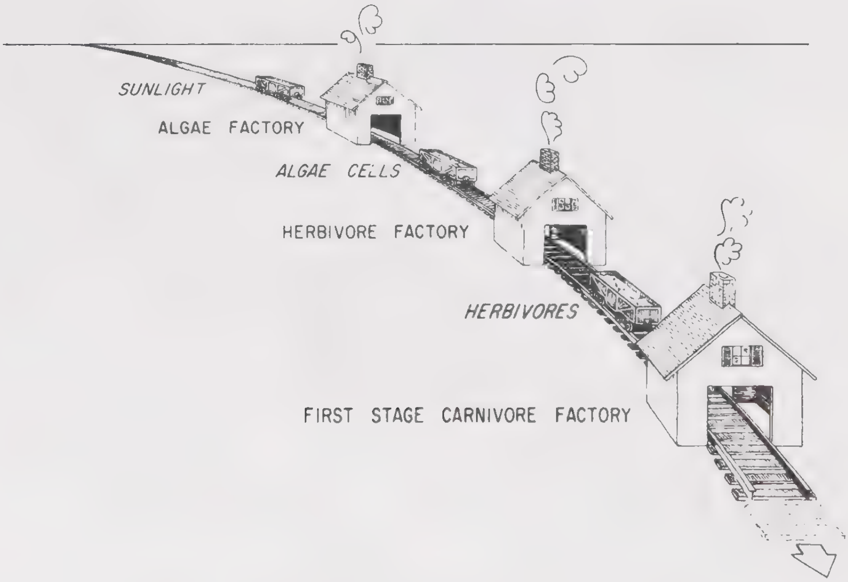

Figure 1. Food chain viewed as a collection of factories.

This food chain approach has actually been used to deduce the total yield of the ocean and portions of the ocean such as the oceanic region. Ryther (1969) discusses the primary productivity of the various ocean regions, the rate of production of the "algae factory." First there is the open ocean or the *oceanic province* which is our major concern today. This province occupies 90 percent of the world ocean. However, its mean primary productivity is rather low (about 50 grams of carbon per square meter per year is fixed in organic matter). Next we have the *coastal zone,* which represents about 10 percent of the total ocean area including offshore areas of high productivity. The productivity is higher here, about 100 grams of carbon per square meter per year. Finally we have the *upwelling areas,* which occupy a fraction of a percent of the total area and have the highest productivity of all—300 grams of carbon per square meter per year. It is significant to note that, even with its low primary production per square meter, the oceanic province represents, according to Ryther's statistics, about 85 percent of the total annual productivity of the sea, yet only 2 or 3 percent of the world fish catch is taken from this area.

Next we need to evaluate the transformation process in each factory. How much material is carried in the boxcars to the next factory and how much is blown out of the smokestacks as metabolites and other material? In discussing the transformation process we will discuss the food chain approach as defined by Ricker (1969). Ricker discusses the two relevant coefficients:

> *E,* the ecotrophic coefficient—the fraction of a prey species' annual production that is consumed by predators (trophic referring to nutritive or food levels);
> *K,* the growth coefficient—the predators' annual increment of weight divided by the quantity of food they have consumed.

Ricker (1969, p. 94) adjusts the ecotrophic coefficient for recycling and arrives at the following values:

	Growth coefficient (*K*)	Ecotrophic coefficient (with recycling adjustment) (*E*)
Primary consumption (grazing on green plants)....	15%	66%
Higher levels	20%	75%

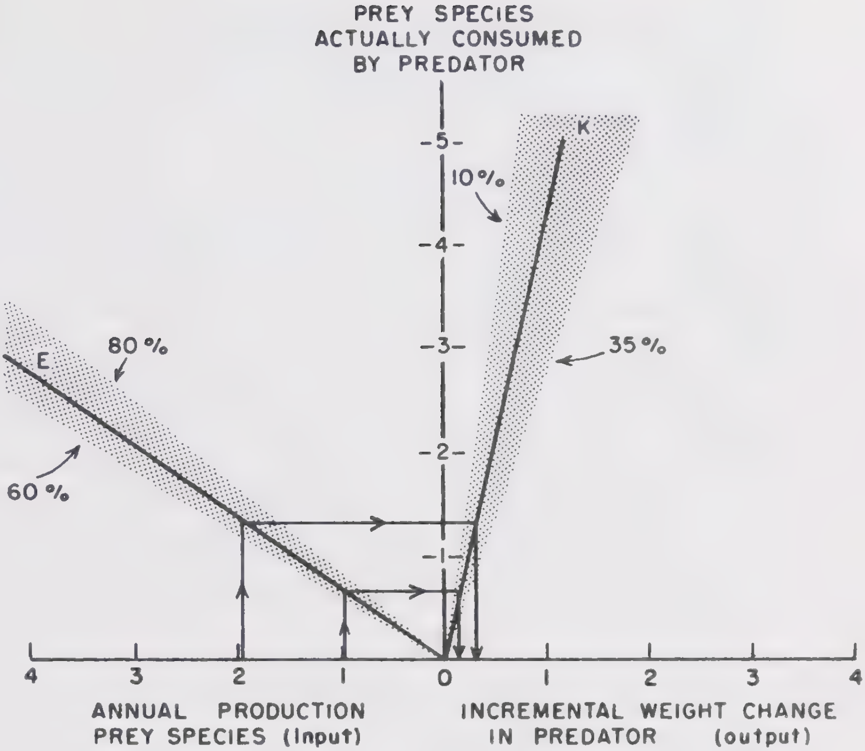
PREY SPECIES
ACTUALLY CONSUMED
BY PREDATOR
-5-
-4-
-3-
-2-
-1-
10%
35%
80%
60%
E
K
4
3
2
1
0
1
2
3
4
ANNUAL PRODUCTION
PREY SPECIES (Input)
INCREMENTAL WEIGHT CHANGE
IN PREDATOR (output)

Figure 2. The relation between the annual production of prey species (input), the prey species actually consumed by the predation, and the incremental change in the production of the predator (output). The two lines which trace the transformation of input to output demonstrate the effect of an incremental change of input on output.

giving *KE* values of roughly 10 percent at the herbivore stage and 15 percent at the higher levels. Figure 2 is a diagram of this process, showing that changes in the production of prey species can have proportionately equal effects on the change in incremental weight of the predators.

Note that by the simple way the problem is formulated, the relation between the ordinate values and the abscissa values must be straight lines passing through the origin, a situation which may be quite unlikely in the real world. This is, of course, true of all constant transfer coefficients that are given in the literature.

Ryther used coefficients, *KE,* of 10, 15, and 20 percent for the oceanic, coastal, and upwelling provinces respectively. The exact magnitude of these coefficients is not at all certain. It is also not clear that they differ in a consistent way between the oceanic, coastal, and upwelling provinces. They may, in fact, be more variable depending on the level of the chain rather than the location of the chain. There is, however, general agreement that the coefficients lie between 10 and 20 percent.

Next we need to know how many factories or levels exist in our simple model. Ryther assumed that harvestable fish production would occur at the fifth trophic level in the oceanic province, at the third in the coastal zone, and between the first and second (1 1/2) in the upwelling zone. This assignment along with the efficiencies provided Ryther with a guess at the total potential production of fish in the world ocean of about 240 million metric tons. His figures give equivalent total fish production to the coastal and upwelling provinces, but allocate 1/150 of the total potential fish production to the oceanic province. In other words, only 10 percent of the world ocean accounts for something like 99 percent of the total potential fish production. These particular results of Ryther's have been criticized in the literature (see Alverson et al., 1970). The criticism boils down to the fact that many plausible alternate coefficients could have been used to obtain strikingly different conclusions.

Why is there a considerable difference in fish production deduced from impressions of the populations (Table 1) and the food chain analysis? For example, the food chain method gives a fish production in the oceanic province of only 1.6 million metric tons. The actual catch (not the production) is actually approaching this quantity, and yet there are rather large stocks as judged by the number of larvae of unexploited scombrids in the oceanic regions, not to mention the squids, deepwater fishes, and others.

Since it is difficult to pinpoint the difficulties, we might examine the model itself. The most sensitive spot in our food chain model is the length of the food chain. To take an example we note that

$$P_n = P_o k^n$$

where P_n is the production at the nth stage, P_o is the primary production, k is the transfer coefficient, and n is the number of stages. Table 2 gives values of P_n for several P_o at various k and n. Clearly, the number of trophic levels, n, affects P_n very strongly. Changes in k appear to be relatively unimportant for most reasonable values of k. Using the above equation for particular areas may give us some idea about the adequacy of the classic food chain model in the regions of interest. As we explore the details of the simple model, we are aware that the divergence between the food chain approach and the extrapolated estimate of oceanic productivity could very well be produced by the model

Table 2. Expected levels of fish production in the oceanic province (derived from food chain model)

Level of primary production	Transfer coefficients (k)								
	20%			15%			10%		
	Trophic levels (n)								
	2	3	5	2	3	5	2	3	5
$gCm^{-2}yr^{-1}$									
50	10	2	0.08	7.5	1.13	0.025	5	0.5	0.005
100	20	4	0.16	15	2.25	0.051	10	1	0.01
300	60	12	1.48	45	6.75	0.153	30	3	0.03

diverging from the real world, a difference in the number of trophic steps which was used for the food chain model, or extrapolations that are too high. It is less likely that the values of the transfer coefficients or the estimates of primary productivity produce these divergences. With respect to realism it is well known that it is extremely difficult to evaluate at which trophic level an animal actually resides. While it is relatively easy to determine what an animal eats, it is not easy to determine what its food ate; in any case, no organism is going to fit into neat integral trophic levels, especially during the course of its life.

Given that the factory model is a very simplified abstraction, we must ask whether it is a satisfactory approximation. It is, in the sense that we can come up with almost any answers by modifying the various coefficients. But this may not be a good criterion. The main utility of such a model will almost certainly lie in enabling us to understand how the fundamental processes in the ocean *differ* from the simple model. Most critical are the pathways and feedback mechanisms that channel the flow of energy among the factories and the inner workings of the factories themselves. Short circuiting of the chain can produce substantial differences in production of animals of harvestable size.

Some of the problems of generalizing about the biology of oceanic fishes with respect to trophic dynamics could be considered in terms of "average" coefficients and trophic levels. It may be that certain species which inhabit particular water masses (see Ebeling, 1967) are characterized by particular sets of coefficients and trophic levels and that the differences in these features among water masses would induce more variability in these characteristics than that which would obtain, for example, for demersal fishes. In addition the "two-layered" tropical ocean produces some intriguing problems in food chain dynamics with respect to introducing nutrient-rich water into the photic zone by eddies downstream of islands (see Barkley, 1972) and by the diurnal migration of some fish between the surface and deep layers.

Another intriguing problem in oceanic food chains, which again involves the question of how we interpret trophic levels, is the role of organic substances and the equilibrium between dissolved and particulate organic material. Exactly how this material is incorporated into the food chain and if it is incorporated in significant amounts remains elusive. Provasoli (1963) has compiled a considerable amount of information on this subject. He emphasizes the difficulties of dealing with organic substances in sea-water which are caused by their minute concentrations: "Characterization of organic compounds in sea-water is complex because the dissolved organic C averages 2 mg/s (maxima up to 20 mg/s). These minimal quantities have to be separated from 35,000 mg of inorganic salts in a liter of sea-water. . . ." These tiny quantities of organic material evidently contribute to the existence of the phenomenon that Provasoli calls "good" and "bad" waters; for example, the ". . . productivity along the coast of California is far less than around the British Isles, yet the phosphate content of California waters is many times higher."

Even though modifications in the transfer function may not be relatively important, it is worth emphasizing the simplicity of the model by pointing out that it does not consider time lags. This is easily demonstrated by examining simple control system equations. The transfer function that is typically used in food chain dynamics is the zero order function:

$$I = k\Omega$$

where I is the output, Ω is the output, and k is a constant. There are quite plausible, more complex functions which can represent the process, viz., the first-order and second-order differential equations:

$$I = k\Omega + L\frac{d\Omega}{dt}$$

and

$$I = k\Omega + L\frac{d\Omega}{dt} + M\frac{d^2\Omega}{dt^2}.$$

A simple unit-forcing function can, depending upon the value of the constants, L and M, generate quite different results for the time-behavior of the output of the system. This is shown in Figure 3.

Thus, with the zero order equation the quantity of material produced at a factory is a constant fraction of the material that enters the factory. With more complex, more realistic equations, there are time

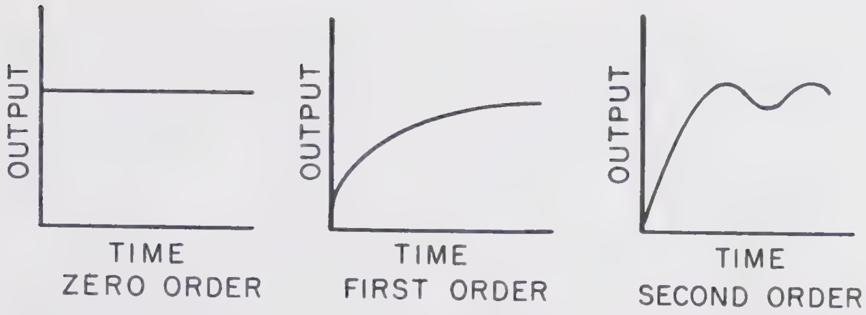

Figure 3. Typical outputs resulting from constant input as a function of time showing different kinds of lag effects possible for zero-order, first-order, and second-order differential equations.

lags which could cause considerable oscillations in the system. (Are these oscillations reflected in varying year-classes of fish?) Another time-related effect is the age effect. Most population theory relates to $dN/dt = zN$, and it can be shown that the average age of the organisms in the population is $1/z$. However, the average age of the population can be modified by changes in the predator population or by fishing. If we assume that size is a function of age, and that diet is a function of size, then the transfer coefficient must be continually changing. The point of this is that the zero order equation is conventionally used, but the higher order equations are much more likely to operate. If, for example, the damping ratio is small, the fluctuations can have yearly or quarterly periods, and the trophic position of organisms must be changing constantly with mortality and other vital rates.

Other factors that affect the nature of the transfer coefficient are various changes in the environment that can be temporary but occur at important stages during the organism's life, and changes of a longer term. Take, for example, the whole question of nutrition (see Phillips, 1969). It is conceivable that there are long-term and short-term changes in the amounts of proteins, fats, and carbohydrates present in a trophic level. The essential amino acids and fats, the sparing action of certain amino acids and fats, and mineral and vitamin requirements may also vary. As another example, consider the fluctuations in temperature that can operate upon an animal's temperature tolerance, preference, "appetite," and digestion. When do these variations of nutrition, temperature, and a host of other factors create significant perturbations in the system? We do not know.

Thus, it is clear that there are many unanswered questions concerning the use of the factory model to forecast the productivity of the oceanic region. Perhaps we need to ask what additional knowledge the food chain model will produce. Perhaps we need to look at some newer configurations of the problem involving the fate and residence time of packets of energy in groups of animals. We could in this context consider a variety of queuing questions for each group of animals: what is the arrival time of packets of energy at different densities and nutritional quality, what are the lengths of the queues, what are the holding times, and what is the effect of queue impatience?

All of this has simply served to point out that the oceanic province is about as little known, with respect to the kinds of information required to make resource decisions, as it was at the time of the *Challenger* expedition. If economic pressures accelerate the harvesting of the oceanic regions, then we need to concentrate upon obtaining information that will promote correct decisions with respect to the exploitation of these resources.

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MFR PAPER 1040

The American eastern tropical Atlantic tuna fleet records its second highest total catch.

Participation by Panamanian and U.S. Seiners in 1972 Tuna Fishery of the Eastern Tropical Atlantic

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ABSTRACT

American participation in the 1972 eastern tropical Atlantic tuna fishery is reviewed. For the American fleet (Panamanian and U.S. seiners) the 1972 season was successful in terms of total catch of 24,200 metric tons of tuna, second highest recorded (highest was the 1969 catch of 24,300 metric tons) since significant numbers of American vessels first participated in the fishery in 1967. Catches, catch rates, fishing areas, and sizes of yellowfin and skipjack tunas caught by the American fleet in 1972 are discussed.

INTRODUCTION

From April through November 1972, 33 American purse seiners[1] fished off west Africa between lat. 30°N and lat. 20°S and east of long. 25°W (the eastern tropical Atlantic). A total of 12,000 metric tons of yellowfin tuna (*Thunnus albacares*) and 12,200 metric tons of skipjack tuna (*Katsuwonus pelamis*) were caught in 3,700 vessel-days of fishing. The total American catch (yellowfin and skipjack) from the eastern tropical Atlantic was 18 percent and fishing effort was 128 percent greater than in 1971. The number of boats, total fishing effort, and length of the season were the highest recorded for the fleet since 1967 when significant numbers of American vessels first participated in the eastern tropical Atlantic tuna fishery (Sakagawa and Lenarz, 1972). A review of the American participation in the 1972 fishery is presented in this report.

TOTAL ATLANTIC CATCH OF YELLOWFIN AND SKIPJACK TUNAS

Preliminary catch statistics, which include principally all significant catches except that of the Taiwanese longline fleet, indicate that the total Atlantic catch (all fleets) of yellowfin tuna in 1972 will exceed the 1971 catch and probably also exceed the all-time high of 92,400 metric tons, which was recorded in 1969 (Figure 1). The increase in the 1972 yellowfin catch occurred primarily in the surface fishery with the American contribution showing improvement from a downward trend which began in 1970 (Sakagawa and Lenarz, 1972).

The total Atlantic catch (all fleets) of skipjack tuna, on the other hand, decreased 18 percent in 1972 from an all-time high of 86,500 metric tons in 1971 (Figure 1). In the American total catch, skipjack and yellowfin tuna contributed about equally, based on weight. This was markedly different from the 79 percent skipjack—21 percent yellowfin composition of the 1971 American catch (Sakagawa and Lenarz, 1972).

MONTHLY CATCHES AND CATCH RATES IN THE EASTERN TROPICAL ATLANTIC

The year 1972 was the first in which the American purse seine fleet entered the eastern tropical Atlantic fishery as early as April. This early entry was largely due to the record early closing (5 March 1972) of the eastern tropical Pacific yellowfin tuna fishery (IATTC, 1973). Most of the 33 American vessels participating in the Atlantic fishery had been in the

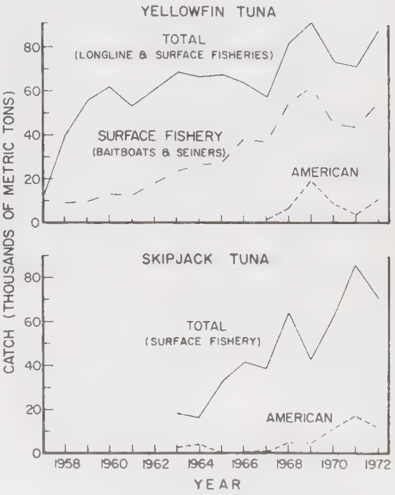

Figure 1.—Total catch of yellowfin and skipjack tunas in the Atlantic Ocean—all fisheries. 1972 figures are preliminary and incomplete.

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[1] American purse seiners refer to vessels flying the flags of Canada, Panama, or the United States. In 1972 no Canadian seiners participated in the eastern tropical Atlantic tuna fishery. The 1972 American fleet consisted of 32 Class 6 vessels (greater than 363 metric tons capacity) and one Class 3 vessel (92-181 metric tons capacity).

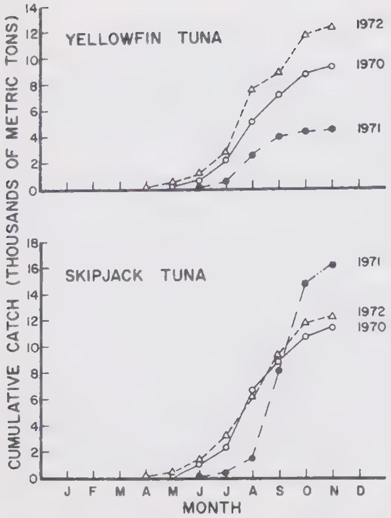

Figure 2.—Cumulative catch of yellowfin and skipjack tunas by the American fleet in the eastern tropical Atlantic, 1970-72.

Pacific yellowfin fishery just before and when it closed. The amount of effort expended by the American

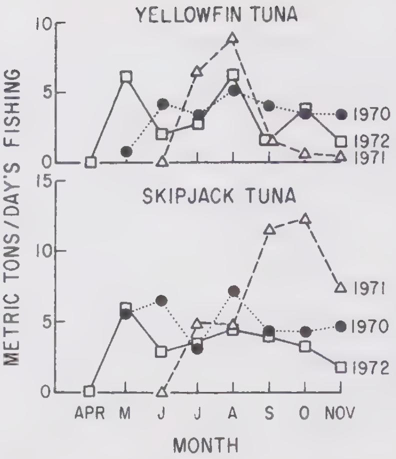

Figure 3.—Monthly catch rates of American seiners in the eastern tropical Atlantic tuna fishery, 1970-72.

fleet in April, however, was too small to be indicative of average fishing conditions for that month; therefore, the catch and catch rate for April are not discussed in this report.

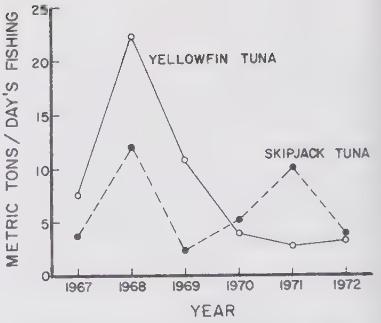

Figure 4.—Annual catch rates of American seiners in the eastern tropical Atlantic tuna fishery, 1967-72.

Although the American fleet entered the fishery earlier in 1972 than in previous years, the pattern of monthly catches of yellowfin tuna followed fairly closely the pattern of 1970, but at a slightly higher level (Figure 2). About 41 percent of the 1972 catch of yellowfin tuna was made in August and 74 percent in the 3

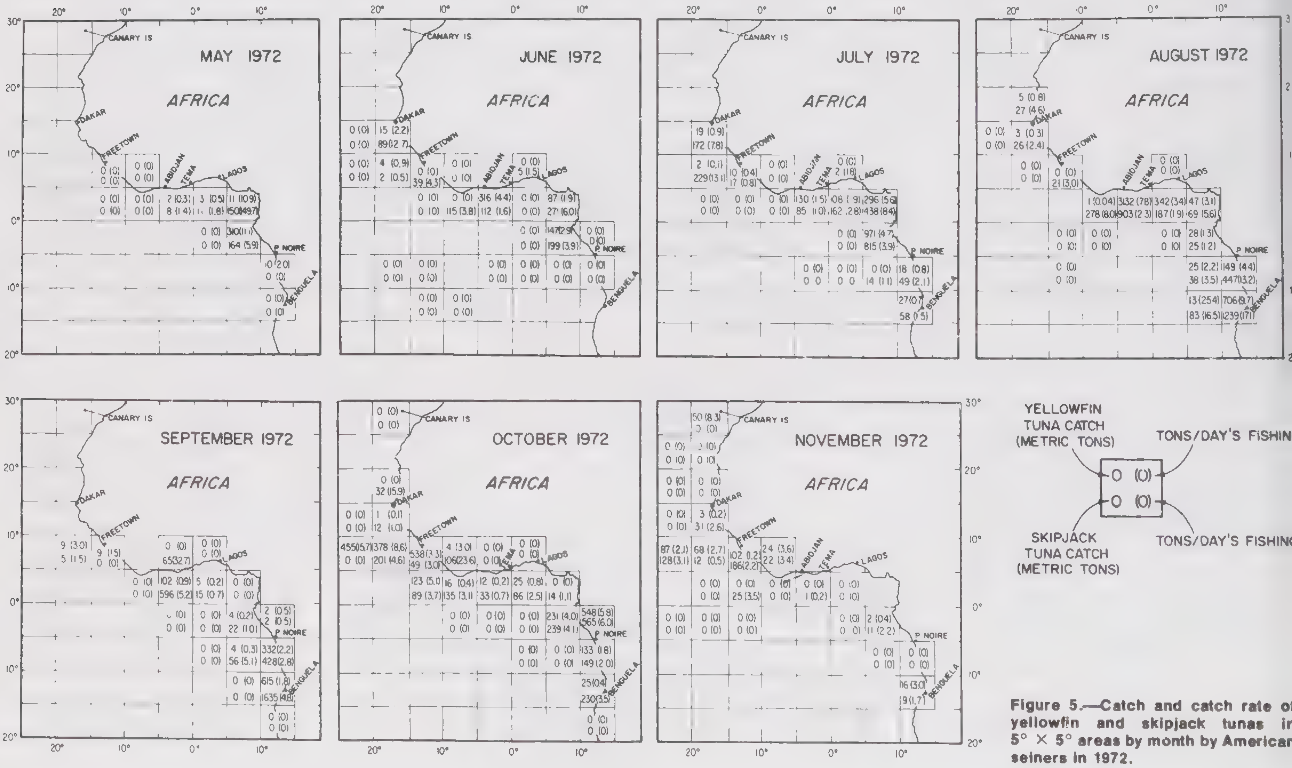
MAY 1972
JUNE 1972
JULY 1972
AUGUST 1972
SEPTEMBER 1972
OCTOBER 1972
NOVEMBER 1972
AFRICA
CANARY IS
DAKAR
FREETOWN
ABIDJAN
TEMA
LAGOS
P NOIRE
BENGUELA
30°
20°
10°
0°
10°
20°
YELLOWFIN TUNA CATCH (METRIC TONS)
TONS/DAY'S FISHIN
SKIPJACK TUNA CATCH (METRIC TONS)
TONS/DAY'S FISHIN
0 (0)
0 (0)

Figure 5.—Catch and catch rate o yellowfin and skipjack tunas i 5° × 5° areas by month by America seiners in 1972.

months, August-October. Fishing for yellowfin tuna was good in May and August (6.1 metric tons/day's fishing) and poor in September and November (1.5 metric tons/day's fishing Figure 3). For the season as a whole the catch rate was 3.3 metric tons of yellowfin tuna/day's fishing, slightly higher than the 1971 rate (Figure 4).

The pattern of skipjack catches was nearly identical to that of 1970 (Figure 2). About 70 percent of the total 1972 skipjack catch was made in August-October. Fishing for skipjack was good in May (6.1 metric tons/day's fishing) and poor in November (1.8 metric ton/day's fishing. Figure 3). For the season as a whole the catch rate was 3.7 metric tons of skipjack tuna/day's fishing, well below the 1971 rate of 10.0 metric tons/day's fishing (Figure 4).

"BEST" FISHING AREAS IN THE EASTERN TROPICAL ATLANTIC

In May-July 1972 the "best" areas of fishing, in terms of high catch rates (considering only 5° × 5° areas in which five or more fishing days were expended in a month), for the American purse seine fleet were generally in the northern part of the Gulf of Guinea for yellowfin tuna and off Portuguese Guinea for skipjack tuna (Figure 5). In August, high catch rates were also obtained in the northern part of the Gulf of Guinea, but the "best" fishing area was off Benguela, Angola (lat. 10°S and long. 10°E), where 9.7 metric tons of yellowfin tuna/day's fishing and 17.1 metric tons of skipjack tuna/day's fishing were caught (Figure 3). In September, the fleet had overall poor fishing, but the "best" skipjack fishing was off Angola (lat. 10°S and long. 10°E), Ghana and the Ivory Coast (lat. 0° and long. 0°), and "best" yellowfin fishing, off Angola. A northward shift in "best" fishing grounds occurred in October and November, with the "best" fishing off Sierra Leone and Liberia (lat. 5°N and long. 15°W) and as far north as the Canary Islands (lat. 25°N and long. 15°W). In October, there was also reasonably good fishing, especially for yellowfin tuna, off Congo and Gabon (lat. 0°S and long. 5°E). A summary of the "best" fishing areas for the American fleet by month for 1972 is given in Table 1.

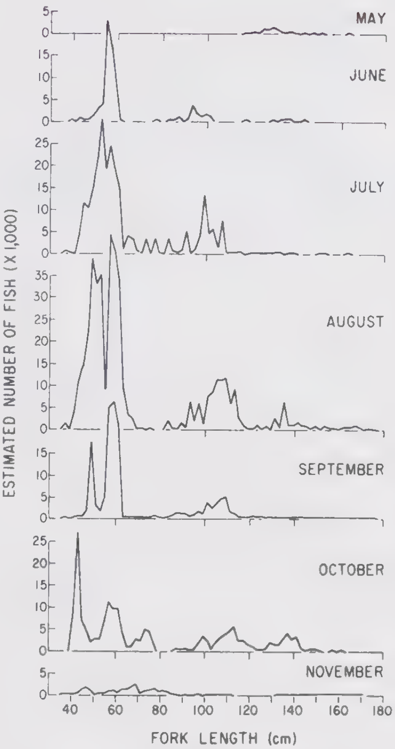

Figure 6.—Length-frequency distributions of yellowfin tuna caught by American seiners in the eastern tropical Atlantic, 1972.

Table 1.—Areas of "best" fishing for American seiners, 1972.

Month	Yellowfin tuna	Skipjack tuna
Apr.	(Insufficient data)	(Insufficient data)
May	Congo	Congo
June	Ghana-Ivory Coast	Portuguese Guinea
July	Gabon	Portuguese Guinea-Sierra Leone
Aug.	Angola	Angola
Sept.	Angola	Ghana-Ivory Coast
Oct.	Liberia-Sierra Leone	Angola; Liberia-Sierra Leone
Nov.	Canary Islands; Liberia-Sierra Leone	Liberia-Sierra Leone

In 1972 some fishing effort was expended at considerable distances offshore (>570 km) but no tunas were caught (Figure 5). The amount of effort, howevever, was small (about 1 percent of total), so the results may not be indicative of the areas' potential as a source of tuna for the surface fishery. More exploration is needed to determine whether the total yield of especially yellowfin tuna might be substantially increased if the surface fishery expanded its operations farther offshore, as occurred in the eastern Pacific yellowfin tuna fishery (Joseph, 1970).

SIZE COMPOSITION OF CATCH

Three age groups of yellowfin tuna were principally caught by the American purse seine fleet in 1972. About 70 percent of the catch in numbers was 1-year-old fish (35-70 cm), 24 percent, 2-year-old fish (71-125 cm) and 4 percent, 3-year-old fish (126-150 cm). July through November were the best months for catching 1-year-old and 2-year-old yellowfin tuna, and May, August, and October were best for

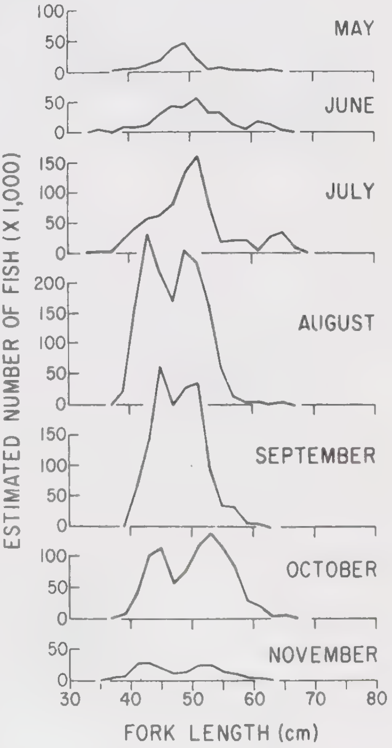

Figure 7.—Length-frequency distributions of skipjack tuna caught by American seiners in the eastern tropical Atlantic, 1972.

catching 3-year-old fish (Figure 6). The average length of yellowfin tuna in the total American catch was 70 cm.

Considerably more skipjack tuna in numbers than yellowfin tuna were caught in 1972 (5.3 million skipjack versus 1.1 million yellowfin). Exploitation was principally on the young-of-the-year (in the size range of 32-55 cm), but some 1-year-old skipjack (about 65 cm long) were also caught (Figure 7). The average length of skipjack tuna in the American catch was 49 cm.

SIGNIFICANCE OF RESULTS

In 1972, the International Commission for the Conservation of Atlantic Tuna (ICCAT) adopted a minimum size limit of 3.2 kg (55 cm) for yellowfin tuna with a provision that incidental catches of yellowfin tuna below this minimum size should not exceed 15 percent of the total yellowfin catch by number. This regulation was slated to begin in 1973, and, therefore, did not affect the 1972 fishery. If such a regulation had been enforced in 1972, as much as 8 percent, or about 1,000 metric tons, of yellowfin caught by the American fleet in that year could not have been landed.

Although fishing effort of the American fleet increased 106 percent in 1972 over that of 1969, the year of the largest American catch of yellowfin tuna (Figure 1), the yellowfin catch decreased 39 percent. The catch rate of yellowfin tuna also decreased from 11 metric tons/day's fishing to 3 metric tons/day's fishing (Figure 4), and the average length of yellowfin in the catch decreased from 122 to 70 cm. Probable causes for this are: variable recruitment strength, e.g., 2-year-olds were the dominant age group in 1969 and 1-year-olds in 1972; shift in spatial-temporal distribution of fishing effort, e.g., since 1970 the fleet has concentrated its effort off Angola during a major part, September and October, of the season; change in availability and/or abundance of skipjack tuna, e.g., 4,400 metric tons or 18 percent of the total 1969 catch and 12,100 metric tons or 50 percent of the total 1972 catch was skipjack tuna; fishermen avoiding the capture of large fish in 1972 because of their high mercury content; or the actual abundance of yellowfin tuna decreased in 1972 within the geographic boundaries where the surface fishery operates.

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SOME CONSIDERATIONS OF FISHERIES DEVELOPMENT PROBLEMS IN THE PACIFIC ISLANDS AREA

by

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INTRODUCTION

Since the termination of World War II in 1945, a substantial amount of effort has been directed toward the development of fishery resources of waters surrounding the thousands of islands in the Pacific (commonly identified as Oceania). Various development projects have been sponsored by the island governments and territories, international agencies, e.g. Food and Agriculture Organization of the United Nations (FAO), South Pacific Commission (SPC), private funding agencies, and private enterprises. References to recent successes have centered around the development of the Pacific-wide fisheries for subsurface tunas and billfishes (Johnson, 1959) and more recently the development of fisheries for skipjack tuna, *Katsuwonus pelamis*, in the western Pacific, principally the Palau Islands region (Uchida, 1970), Papua New Guinea (Kearney, 1973), and the extensive southern water Japanese skipjack tuna fishery (Tohoku Regional Fisheries Research Laboratory, n.d.). Attempts to develop new coastal fisheries or to expand existing fisheries of the neritic-pelagial resources have met with varying success. One of the remarkable successes has been that of the fishery for round scad, *Decapterus* spp., in the Philippines, a fishery which increased from an annual catch of 19.0 thousand metric tons in 1956 to 206.8 thousand metric tons in 1967 (Shomura et al., 1971).

There have been failures in fisheries development programs; however, these are more difficult to identify since failures generally are not publicized nor well documented. The scope of these failures ranges from small projects designed to aid subsistence-type fisheries to developmental projects involving substantial capital. An example of the latter is the attempt by private enterprise in the 1940's to develop a tuna fishery in American Samoa. A cannery was constructed with the objective of obtaining an adequate supply of surface schooling tuna from Samoan waters. For several reasons, the principal one perhaps being the lack of an adequate supply of baitfish, the expected catch of tuna did not materialize and the project failed. Interestingly, the cannery was put into use a decade later utilizing subsurface tunas caught by Japanese longline vessels (Van Campen, 1954).

In the following sections, I will comment on a number of areas which need to be considered in undertaking a fisheries development program. The discussion is far from comprehensive and should be viewed as providing some of the ingredients for a total systems package. Many of my comments are simplistic and obvious, but in view of the shortcomings of many fishery development projects, past and present, it may be useful to make these comments.

GOVERNMENT POLICY

A positive fisheries policy by a government is essential if a fisheries development program is to succeed. This is especially critical in the Pacific islands area where development programs usually commence from a starting base beset with potential difficulties, e.g. lack of qualified help, problems in logistics, and absence of proper infrastructure.

In developing a fisheries policy and a subsequent program, the government is initially dependent upon advice obtained internally from its staff or externally from experts and consultants enlisted from elsewhere. Ideally, the government needs an initial overview of the total fisheries picture, including the assessment of naturally occurring fishery resources, and evaluation of aquacultural possibilities, marketing potential, required infrastructure for fishery development, and a "first cut" economic analysis. In essence, a systems analysis approach such as described for fishery management by Rothschild (1971) is required for the development of a sound fishery policy and program. In describing a systems approach, Rothschild (1971) states "The central theme in systems analysis involves using the anlysis to ask the right question by cycling iteratively through (1) defining objectives, (2) designing alternative systems to achieve these objectives, (3) evaluating the alternatives in terms of costs and effectiveness, (4) questioning the objectives and other assumptions underlying the analysis, (5) using this examination to open new alternatives, and (6) establishing new objectives. Once the new objectives are established, the cycle is re-entered at step (1)...." Successful planning should result in program priorities being established on the basis of knowledge of the fishery resources available, and development should be in line with the objectives of the government, e.g. increasing domestic consumption of fish and fishery products, establishing a more favorable foreign exchange by developing export markets, or increasing job opportunities.

It is unfortunate that in some areas, decisions on program support have been based on recommendations made by experts in specialized fields without examining alternatives to achieve the primary objectives. Within the context of the specialized fields, e.g. aquaculture, turtle farming, outer reef fishing, or bottom trawling, the priorities and recommendations expoused by these specialists may be sound; however, without reference to the country's objectives some poor decisions have been made and low priority programs have been funded at the expense of needed programs. Considering the small budgets usually associated with fisheries departments, it is essential that the decision makers address the question of "are you doing the right thing or doing the thing right?"

RESOURCE PROBLEMS

In the development and management of fishery resources, Gulland (1971a) noted that policy makers need three sets of figures: the best current estimates of the potential sustained yield from the stock, the present catch, and plans for increase in catch. For much of the area under consideration (principally the volcanic and coral islands of Oceania) these figures are virtually lacking. Even in Hawaii where the state government has a routine system of collecting commercial catch statistics, the reported catch is considered to be an underestimate of the true landings; this is principally because the recreational catch, which is estimated to be substantial, goes unreported.

Gulland (1971b) in a review of the fish resources of the ocean provided rough estimates of the potential yield of fishery resources (excluding tunas and billfishes) around the volcanic and coral islands of the western central Pacific (included are Nanpo Shoto group, Trust Territory of the Pacific Islands, Gilbert Islands, Ellice Islands, Solomon Islands, and the islands southeast of Papua New Guinea). For this area, Gulland estimated the yield to be around 43,500 tons and suggested that a three to fivefold increase of this minimum figure was not unrealistic as representing the true potential yield. Compared to the potential yield estimates of other underutilized resources, e.g. 2 million tons estimated for the California anchovy, Engraulis mordax, (Gulland, 1971b), the resources of the island waters do not suggest having the base necessary to sustain large scale fisheries. This does not, however, include the skipjack tuna resource, which is reported to be a large underutilized resource in the Pacific (Matsumoto, 1974). Murphy (1973) stated that "...a Pacific Islands fisheries program is not likely to contribute greatly to the world's fish supply."

Gulland (1971a) and Murphy (1973) stress the need for stock assessment estimates for rational development and management of the resources. While gross estimates of potential yields have been attempted for the Pacific island areas, these are "educated" guesses, at best. Although indications all suggest that the fishery resources of the coastal waters of the Pacific islands are only large enough to support fisheries for domestic needs, and at best a modest export industry, e.g. spiny lobsters, stock assessments are needed for proper management purposes. Murphy (1973) noted that one of the basic problems hindering stock assessments in the tropics is our inability to age tropical fish. Since publication of his paper, however, there has been a breakthrough in this problem area; recent studies provide evidence that fish otoliths bear markings representing daily growth increments. Current studies on the Hawaiian anchovy, Stolephorus purpureus, skipjack tuna, and goatfish, Mulloidichthys samoensis, in Hawaii are substantiating the validity of this aging technique (Paul Struhsaker, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. comm.)

Stock assessment studies of tropical fishery resources are also needed to clarify the turnover rates of production. One of the prevailing views is that tropical waters do not have a high standing crop of biological entities, vis à vis waters of higher latitudes; however, it is believed that a presumed faster growth rate, earlier maturation, and shorter life span provides for a rapid turnover rate in tropical waters and thus a high potential annual yield. As an example, the life span of the California anchovy and Japanese anchovy, Engraulis japonicus, is measured in terms of several years; the Hawaiian anchovy, on the other hand, has a reported life span of about 6 months (Paul Struhsaker, pers. comm.).

One of the principal deterrents in the development of fisheries for large scale local market operations or export fisheries in the Pacific islands areas is the large number of fish species encountered. The fish fauna is basically of Indo-Pacific origin and highly varied. In Hawaii, the fish fauna is reported to number 682 species (Robert T. B. Iversen, Southwest Region, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. comm.); a considerable number of these species appear in the fresh fish markets. For most large-scale fisheries the industry is generally geared to a few species, e.g. Peruvian anchovy, Norwegian herring, Alaska pollock, tunas and salmon. In a number of fisheries where many species are taken in addition to the principal species sought, e.g. shrimp trawl fisheries, the fish taken as byproduct are considered of nuisance value and are often discarded. The reasons are basically economic in nature with the cost of sorting, handling and marketing not commensurate with the potential earnings. Another complicating factor is that the catches made by the types of gear used in the coastal waters of the Pacific islands, e.g. traps, gill nets, and handlines, cover a wide range of fish size.

The widespread distribution of the fishing grounds also retards further development of existing fisheries or the establishment of new fisheries. Except for the islands in the far western Pacific, e.g. Philippines and Indonesia, where the fishing grounds are extensive and geographically concentrated, islands of the Pacific have narrow shelves; thus the habitat for a given species or group of species is limited in size and usually strung out along island chains extending over great distances. In the Hawaiian archipelago, the grounds between 0 and 100 fathoms are estimated to be 20,800 km^2 in area; however, these grounds are distributed over a horizontal distance of 1,660 nautical miles.

Finally, in the resource problem area is the presence of ciguatoxin in some reef fishes. The lack of a rapid method of detecting ciguatoxin in fishes has forced fishermen to discard those species noted to have a history of toxicity. In some developing fisheries this amounts to a considerable percentage of the catch. In American Samoa a viable handline fishery was started in 1972. In recent years the annual landed catch has totaled around 136.1 thousand kg; an approximate 27.2 to 45.4 thousand kg of fish have been discarded because of potential problems (Stanley N. Swerdloff, Office of Marine Resources, Government of American Samoa, Pago Pago, American Samoa 96920, pers. comm.). This discard represents a substantial economic loss to the fishermen.

PEOPLE PROBLEMS

Basically the people problems in fisheries development involve the difficulty of placing the right people in the right places at the right time. The failure of some fisheries development programs can be directly traced to the disruption of the time phases of the program because of personnel problems, e.g. the lack of qualified mechanics at the start of a developing fishery is crucial to success of the fishery, since mechanical difficulties result in reduced fishing time; a reduction that fishermen in a developing fishery can ill afford.

In some development programs which involve on-site training of local talent, staffing is often inadequate. The failure of some development programs can be attributed to this lack of "critical mass." Presently there are a number of programs being carried out in the central and western Pacific Ocean to develop skipjack tuna fisheries, e.g. in American Samoa, Western Samoa, Trust Territory of the Pacific Islands and Fiji. Considering the complexity of a pole-and-line fishery, a fishery which involves fishing for baitfish, fishing for tuna, and operating and maintaining relatively large vessels, most of the programs appear to be undermanned in terms of qualified personnel.

In many areas of the Pacific Ocean a common complaint expressed is that many of the island people do not have extensive fishing traditions and thus cannot be counted upon to take an active role in the producer (fishing) end of the industry. While this may be true for some of the more arduous types of fishing, e.g. longline fishing with its long hours of work and long periods away from home port, many of the coastal types of fishing represent viable vocational options to the peoples of the Pacific islands.

In reviewing the shortcomings of past attempts to provide local input into developing fisheries, several points should be considered. First is that the social and economic structures of many areas are not as highly time-oriented as in many of the western cultures. In an industry where each member of a fishing crew is closely dependent upon the other, the tardiness or absence of one man can cause serious problems. Motivation is also a vital consideration. The economic level in many of the areas is such that economic motivation--the desire to accumulate capital (cash)--may be lacking. Until the economy progresses from basically subsistence to a cash economy, the motivational problem will probably continue to exist. The socio-economic aspects of fishery development in the Pacific island areas have not received adequate attention.

Similar to the problem of the geographically widespread resources noted in an earlier section, the companion problem of the widespread distribution of people and facilities also handicaps development of fisheries in the Pacific islands area. Recently there have been some attempts to overcome this problem by setting up a series of holding facilities on scattered islands and sending mother ships to collect the catch at intervals. Success of this method of development will depend on the economics of the system.

DISCUSSION

Despite the multitude of problems associated with developing fisheries in the Pacific islands area, the case is not a hopeless one. In fact, from a resource utilization standpoint it is essential that fisheries development work continue in this area. As the populations increase and the island territories and governments expand their economies, the trend towards urbanization will continue. Thus, while many of the areas are currently able to meet their protein needs through subsistence fishing, the demand for expanded domestic fishing and for the development of high-seas fisheries is bound to increase in the coming years. Needed are sound fisheries objectives by governments which are consonant with the available fishery resources within their region. Alternatives need to be examined, infrastructure problem areas need to be anticipated, and socio-economic aspects need to be considered. In essence there is a need for a total systems analysis package.

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Mercury in Several Species of Billfishes Taken Off Hawaii and Southern California

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ABSTRACT

The results of analyses of the mercury content of 37 blue marlin, *Makaira nigricans*, 56 striped marlin, *Tetrapturus audax*, and 3 swordfish, *Xiphias gladius*, are presented.

The levels of total mercury found in white muscle of blue marlin caught in Hawaiian waters ranged from 0.19 ppm to 7.86 ppm; fish specimens ranged in total weight from 96 pounds (43.5 kg) to 906 pounds (410.9 kg). A trend of increasing mercury level with increasing size of fish was noted. The mercury content in the livers of 26 blue marlin specimens examined ranged from 0.13 ppm to 29.55 ppm; there was no apparent trend noted between mercury content in the liver and size of fish.

Striped marlin from Hawaii and southern California showed a range of mercury levels in white muscle of 0.09-1.09 ppm for the 14 Hawaii samples examined and 0.03-2.1 ppm for the 42 California samples examined. The range in size of fish was 56-139 pounds (25.4-63.0 kg) and 109-231 pounds (49.4-104.8 kg) for the Hawaii and California samples, respectively. From the wide spread of mercury levels encountered in striped marlin, a trend of mercury level with size of fish could not be easily detected. Livers of nine specimens from the Hawaii catch were analyzed; mercury levels ranged from 0.05 ppm to 1.53 ppm.

Three swordfish weighing 6 pounds (2.7 kg), 100 pounds (45.4 kg), and an estimated 500 pounds (226.8 kg) contained mercury levels in white muscle of 0.04, 1.71, and 2.10 ppm, respectively.

In early December 1970 the news media stunned the nation, particularly the fishing industry, with the release of stories that some canned tuna and swordfish steaks contained mercury in excess of the Food and Drug Administration (FDA) interim guideline of 0.5 ppm (Bernstein, 1970; Fleming, 1970; Los Angeles Times, 1970; Coffey, 1971). Prior to State University of New York Professor Bruce McDuffie's discovery that mercury levels in two cans of tuna exceeded the FDA guideline, the problem of mercury in fishes was thought to be localized and confined to freshwater fish species. The high levels of mercury in freshwater fishes were attributed to dumping of waste products into waterways.

A review of the literature undertaken at the time of the announcement of mercury in tuna and swordfish revealed a wealth of information related to mercury and its toxic properties; references were primarily of incidents occurring in Japan and Sweden. Despite the wide range of available information, there was a conspicuous lack of data related to mercury levels in living organisms in the marine biosphere. For this reason the National Marine Fisheries Service embarked upon an extensive program early in 1971 to collect tissue samples of marine and estuarine fishes and invertebrates for analysis of mercury and other heavy metals (Commercial Fisheries Review, 1971).

Primarily because of their recreational value, the California Department of Fish and Game collected samples of striped marlin, *Tetrapturus audax*, and albacore, *Thunnus alalunga*, for mercury analysis during the summer of 1971.

Our purpose in this paper is to provide the results of analysis for total mercury content in samples of striped marlin, blue marlin, *Makaira nigricans*, and swordfish, *Xiphias gladius*. We will simply present these data with some brief comments of the more

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notable features. It is not our intention to review the instances of mercury poisoning, the legal aspects of the mercury guideline, nor the issue of natural versus pollution-caused heavy metal contamination.

MATERIALS AND METHODS

Of the 56 striped marlin sampled, 42 were caught off southern California, while the remaining 14 were from Hawaiian waters. All of the 37 blue marlin and 2 of the 3 swordfish were from Hawaiian waters. One small (2.7 kg) swordfish was caught with longline gear in the central equatorial Pacific. The recreational fishery provided all the California samples; data and tissues were collected either at the weighing facilities of the Balboa Angling Club or the Marlin Club of San Diego. The Hawaii samples consisted of fish caught by the commercial longline fleet and by the troll sport fishery. The commercial catch was sampled at the Honolulu fish auction, while the sport catch was from fish caught during the 1971 Hawaiian International Billfish Tournament held at Kailua-Kona, Hawaii.

With the exception of the small swordfish which was preserved in Formalin,[3] all of the samples were collected from fresh, unfrozen specimens. From ½ to 1 pound (0.23 to 0.45 kg) of white muscle tissue was excised from each fish. In the California striped marlin samples, the tissue was removed from the dorsal loin above the left pectoral fin. Nearly all the Hawaii samples came from near the caudal area because this portion is usually discarded after a buyer has purchased the fish from the auction market. In all cases the tissue sample was cleaned of skin and bone, wrapped in inert aluminum foil, labeled, and then frozen as soon as possible. After the samples had been collected they were packed in Dry Ice and shipped to the analytical laboratories by air. Liver tissue from 4 Hawaiian striped marlin and 26 blue marlin also were collected for comparative analysis.

The Hawaii samples were analyzed at a National Marine Fisheries Service Laboratory while those from California were done by a Department of Fish and Game Laboratory. In 17 of the California striped marlin sampled, muscle tissues were sent to each of the analytical laboratories.

Similar laboratory procedures were followed in all cases; this consisting basically of the semiautomatic, cold vapor, atomic absorption technique (Uthe, Armstrong, and Stainton, 1970). This technique requires a lengthy process of homogenizing, digesting, etc., prior to obtaining a total mercury value from the atomic absorption apparatus.

RESULTS

Striped Marlin

Our study covered a relatively wide size range for this species; the smallest weighed 56 pounds (25.4 kg) and the largest 231.5 pounds (105.0 kg). Generally, the larger striped marlin were from southern California while the smaller fish were from Hawaii. Total mercury values averaged 0.8 ppm and ranged from a low of 0.03 ppm in a 135-pound (61.2 kg) fish to 2.1 ppm in a 231.5 pound (105.0 kg) fish, the largest sampled (Fig. 1). Seventy percent or 42 fish exceeded the FDA guideline of 0.5 ppm. A trend line calculated for these data indicates a general increase in total mercury with increasing size of fish. However, as Figure 1 indicates, the increase is erratic and impossible to predict. While the largest fish resulted in the highest mercury content, it is well to note that the second largest, a 218 pounder (99.0 kg), was tested at 0.29 ppm, a figure well below the FDA guideline.

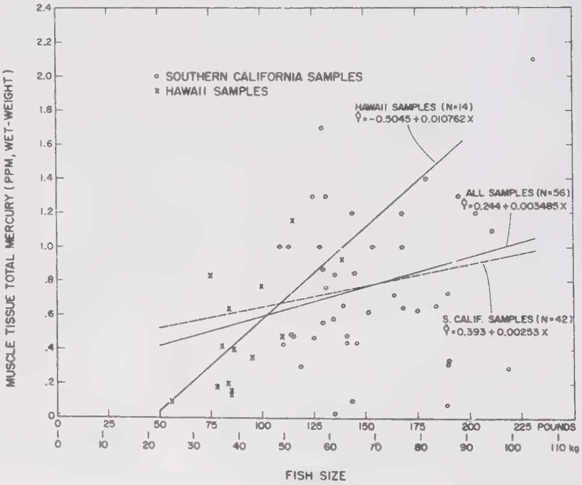

Figure 1.—Relationship between total mercury (ppm) in white muscle tissue and size of fish of striped marlin from southern California and Hawaiian waters.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1.—Comparison of mercury levels in striped marlin tissues analyzed by two laboratories.

	Laboratory no. 1	Laboratory no. 2
Mean HG	0.77 ppm	0.84 ppm
Standard deviation	0.35	0.50
>0.5 ppm	15 fish	12 fish
<0.5 ppm	2 fish	5 fish
High value	1.0	2.1
Low value	0.4	0.1

Some of this variability may be due to analytical technique for it should be remembered that different laboratories provided the analytical data. While analytical methods were being developed there appeared to be considerable variability between laboratories, although the reproducibility within a given laboratory was very high. Our data from the 17 samples that were run by two of the laboratories tend to bear out this feature. Extreme values were repeatable within both laboratories, but there were differences between the laboratories. These differences are illustrated best in tabular form (Table 1).

Looking at individual samples, one laboratory was not consistently high or low and no two values for a particular fish were identical. In several instances one laboratory reported mercury values over the FDA guideline while the other was below. Again, neither laboratory was consistent in this respect.

The livers from four Hawaiian fish also were analyzed for total mercury. Mercury levels of the three small fish (81, 83, and 96 pounds—36.7, 37.6, and 43.5 kg, respectively) were all less than 0.2 ppm, but the single large fish of 139 pounds (63.0 kg) had a value of 1.54 ppm.

Blue Marlin

The mercury data for all the blue marlin were from fish taken in Hawaiian waters. Total mercury levels of white muscle tissue in this species ranged from 0.7 ppm to 7.86 ppm in fish weighing between 96 and 906 pounds (43.5 and 410.9 kg). The results are presented in Figure 2. When compared to striped marlin, the mercury levels in blue marlin were much higher. Only 7 of the 37 blue marlin tested had levels less than 1.0 ppm, while for striped marlin 45 of the 56 fish tested were below that level. The highest value recorded for blue marlin was 7.86 ppm which, surprisingly, was not from the largest specimen, but from a fish weighing 211 pounds (95.7 kg).

As with striped marlin, the range in mercury level for blue marlin is large. However, there appeared to be an indication of a positive relationship between mercury level and fish size when a regression was fitted to the data (Fig. 2). Again, this relationship shows a wide variation around the regression. We would find it difficult to use these data for predicting mercury content in a given specimen.

For comparative purposes we have plotted the linear regression presented by Rivers, Pearson, and Schultz (1972) for blue marlin samples from Hawaiian waters. Since many of the same fish tested by Rivers et al. (1972) were included in our study, we can only conclude that the marked difference in regressions is due to differences in analytical technique. There is agreement, however, that the levels of mercury in blue marlin are considerably higher than the FDA guideline.

The livers of 26 blue marlin also were analyzed for total mercury. The values ranged from 0.13 ppm

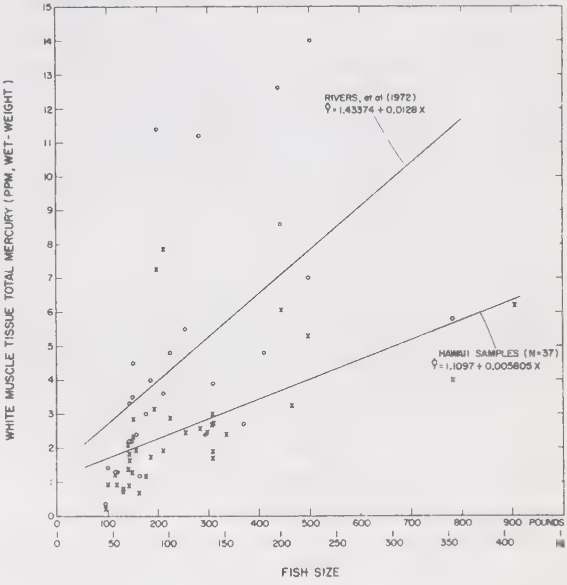

Figure 2.—Relationship between total mercury (ppm) in white muscle tissue and size of fish of blue marlin from Hawaiian waters. (o denotes Rivers et al. (1972) samples, x denotes our samples.)

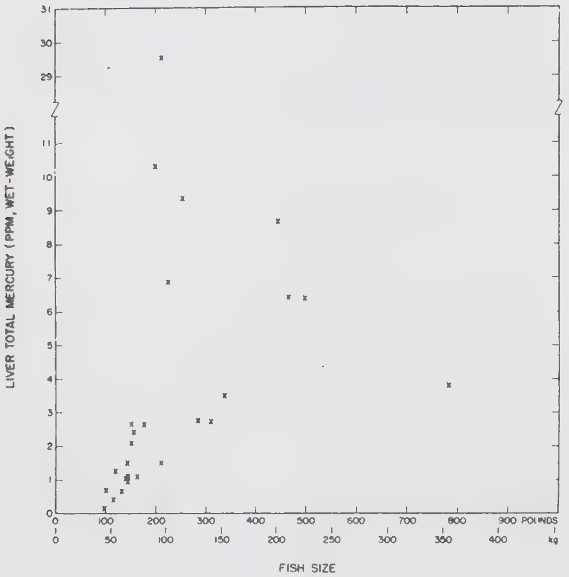

Figure 3.—Relationship between total mercury (ppm) in liver tissue and size of fish of blue marlin from Hawaiian waters.

to a phenomenal 29.55 ppm (Fig. 3). Based upon published literature the latter may be the highest level of total mercury reported for any fish. Coincidentally, this high value was from the same 211-pound (95.7-kg) fish whose white muscle tissue contained the extremely high level of 7.86 ppm total mercury. There does not, however, appear to be a consistent relationship between total mercury content in livers and the content in white muscle tissues.

Swordfish

Only the muscle tissue from three swordfish was analyzed for total mercury. The mercury level in a juvenile swordfish weighing 6 pounds (2.7 kg), which had been preserved in Formalin, measured 0.04 ppm. The analyses from two other fresh specimens from Hawaiian waters weighing 100 pounds (45.4 kg) and 500 pounds (226.8 kg), were 1.7 and 2.1 ppm total mercury, respectively.

DISCUSSION

Results of this investigation may be considered a contribution to the fund of information pertaining to this controversial subject. Confirmation of high mercury levels in billfishes and the relationship of mercury to size, sex, or other variables will require further study.

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Length-Weight Relationships for Six Species of Billfishes in the Central Pacific Ocean

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ABSTRACT

Weight-length relationships for six species of billfishes in the central Pacific Ocean were developed by analyzing 20 yr of data. Log-linear and nonlinear statistical models were fitted to the data by regression analysis, and residuals from the models were tested. Blue marlin, *Makaira nigricans* Lacépède, (50-135 cm FL), male blue marlin (≥135 cm FL) and sailfish, *Istiophorus platypterus* (Shaw and Nodder), apparently have coefficients of allometry less than 3.0. Black marlin, *M. indica* (Cuvier) and female blue marlin (≥135 cm FL) apparently have coefficients equal to 3.0. Shortbill spearfish, *Tetrapturus angustirostris* Tanaka, striped marlin, *T. audax* (Philippi), and swordfish, *Xiphias gladius* Linnaeus, apparently have coefficients greater than 3.0.

As with most studies on the length-weight relationship, this study is not an end in itself. It was initiated to provide length-weight conversion relationships (Equation 1) for use in a growth paper on blue and striped marlins (Skillman and Yong[2]), as well as to provide conversion charts for the sport fishermen at the Hawaiian International Billfish Tournament. There are few published papers on the weight-length relationship of billfishes[3] (de Sylva, 1957; Royce, 1957; Kume and Joseph, 1969); hence, we decided to calculate this relationship for all six species of billfishes on which data had been collected by the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service. These six species were the black marlin, *Makaira indica* (Cuvier), blue marlin, *M. nigricans* Lacépède, sailfish, *Istiophorus platypterus* (Shaw and Nodder), shortbill spearfish, *Tetrapturus angustirostris* Tanaka, striped marlin, *T. audax* (Philippi), and swordfish, *Xiphias gladius* Linnaeus.

Although all of the length-weight data collected on billfishes from 1950 to 1971 by the Honolulu Laboratory were used, this study should not be considered exhaustive or definitive. Even in the best represented species, there were too few data to separate the data according to sex, maturity, and season as suggested by Le Cren (1951) and Tesch (1968). Thus, it was impossible to perform a detailed analysis of covariance similar to that performed recently by Brown and Hennemuth (1971) on haddock, *Melanogrammus aeglefinus* (Linnaeus). Some species were so poorly represented that the length-weight relationships should be considered as tentative relationships.

In general, fishery biologists have accepted the appropriateness of the allometric growth equation (Huxley and Teissier, 1936) or its mathematical equivalent, the power function, as a descriptor of growth in weight to growth in length. We accepted the general form of the relationship (Equation 1) and applied both the log-linear and the nonlinear statistical

$$W_i = b_1 L_i^{a_1} \tag{1}$$

models of the relationship. Each model is discussed, and statistical procedures for evaluating the goodness of fit are presented. Papers by Glass (1969), Pienaar and Thomson (1969), and Hafley (1969) are particularly relevant to this discussion.

MATERIALS AND METHODS

Collection of Data

The data used in this report came from three sources. In nearly all of them fork length (FL) measurements were taken to the nearest centimeter

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[2] Skillman, R.A., and M.Y.Y. Yong. Growth of blue marlin, *Makaira nigricans* Lacépède, and striped marlin, *Tetrapturus audax* (Philippi) in the north central Pacific Ocean by the progression of modes method. Manuscript. National Marine Fisheries Service, Southwest Fisheries Center, Honolulu, HI 96812.

[3] The term billfishes, as used in this paper, includes swordfish.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.

from the tip of the snout to the fork of the tail. Where naris or eye-orbit fork length measures were given, conversion to FL was performed with equations given by Royce (1957). All weight measurements were taken to the nearest pound and were converted to kilograms before analysis.

Two of the data sets were derived from longline catch records taken by research vessels of the Honolulu Laboratory while fishing in central Pacific waters, mostly near the equator. The first of these data sets (deck 1) was obtained from a morphometric study of billfishes by Royce (1957) that was carried out on a series of longline cruises in 1950 to 1953. The second data set (deck 2) was obtained from routine information collected from longline-caught fishes for the years 1950 to 1971. These two longline data sets were combined in the subsequent analyses because they represent the same type of data, though they were collected for different reasons and, in general, do not overlap in time. The last set of data (deck 3) was collected by personnel of the Honolulu Laboratory from fish caught by trolling between 1962 and 1971, in June (once), July, or August during the Hawaiian International Billfish Tournament held in Kailua-Kona, Hawaii (Table 1). Since the five species other than blue marlin were represented in such small numbers in the sample, they were pooled with the longline data. For blue marlin, the trolling-derived data were analyzed separately from the longline-derived data. The longline data represent a pooling over all seasons of oceanic-caught fish while the trolling data represent only inshore catches during the summer months.

All three data sets for most species contained some determinations of sex and maturity, but only the trolling data (deck 3) for blue marlin contained enough information to allow an examination of the sexes separately. All other species and pooled data sets were examined without regard to the sex of the individuals.

Analysis

The goal of this paper was to obtain length-weight relationships for each species by using a statistical model that fitted the data best. To accomplish this goal, the steps listed below were followed:

1. The data were checked for different growth stanzas by plotting the natural logarithms of weight against the natural logarithms of length.
2. Length-weight relationships using log-linear regression for weight on length were obtained for all species.
3. The normality of the error terms was tested for those species that had enough data to perform the tests.
4. The log-linear relationships were tested for their significance.
5. Length-weight relationships using nonlinear regression of weight on length were obtained for blue and striped marlins.
6. Statistical tests were performed to determine whether the log-linear or the nonlinear model was more appropriate.
7. The coefficients of allometry were tested to see if they were different from 3.0.

In subsequent paragraphs, brief discussions will be given regarding adjustments made for the amount of data available for each species, the statistical models themselves, the criteria used to determine best fit, and certain test statistics employed in the analysis.

As can be seen from Table 1, the amount of data available for most of the species for any data deck was very small. Even after pooling all of the data for the black marlin, sailfish, shortbill spearfish, and swordfish, there were too few data to evaluate the fit of the statistical models. Hence, the most commonly used statistical model, the log-linear, was fitted to these species. Only the significance of the relationships was tested. For striped marlin after pooling all data, there were enough data to evaluate the fit of the statistical models. In the analysis of blue marlin, the data were not pooled because we believed that the longline- and troll-derived data represented different biological situations. The longline data were obtained from a sampling program that neglected any seasonally varying and sexually different length-weight relationships, whereas the troll data were obtained in the summer season for each sex. To aid in the interpretation of the striped marlin data, the blue marlin data were pooled for comparative purposes only. There were enough data to evaluate the fit of the models for all blue marlin data categories.

As mentioned in the introduction of this paper, fishery biologists, in general, have accepted the appropriateness of the allometric growth equation as a descriptor of the growth in weight to the growth in length of fish. As expressed by Equation 1, this equation is mathematically a functional relationship (Madansky, 1959) where weight is known exactly

Table 1.—Number of observations by species, by year, by data deck, where deck 1 is from Royce (1957), deck 2 is the Honolulu Laboratory's longline punch card deck, and deck 3 is from the Hawaiian International Billfish Tournament.

Species	Year 1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	Total
Black marlin																							
Deck 1	—	—	—	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Deck 2	—	—	—	—	3	2	3	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	9
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	2	—	2	1	—	—	8
Pooled 1, 2, 3	—	—	—	4	6	2	3	—	—	—	—	—	1	2	—	—	3	—	2	1	—	—	24
Blue marlin																							
Deck 1	—	—	8	19	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	35
Deck 2	—	—	4	17	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	35
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	23	17	29	45	24	63	34	31	85	34	385
Pooled 1, 2	—	—	12	36	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	70
Sailfish																							
Deck 1	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Deck 2	—	—	1	7	3	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	13
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2
Pooled 1, 2, 3	—	—	2	7	5	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	—	18
Shortbill spearfish																							
Deck 1	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
Deck 2	—	—	1	2	—	1	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Pooled 1, 2, 3	—	—	3	5	—	1	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	16
Striped marlin																							
Deck 1	—	—	5	2	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14
Deck 2	1	—	1	1	4	—	5	—	—	—	1	—	—	1	—	—	2	12	—	—	—	—	28
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2	1	4	—	2	—	11
Pooled 1, 2, 3	1	—	6	3	11	—	5	—	—	—	1	—	—	2	1	—	4	13	4	—	2	—	53
Swordfish																							
Deck 1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Deck 2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—	7
Deck 3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pooled	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—	7
Total	1	—	23	56	42	4	14	—	—	—	2	—	24	21	30	45	31	82	40	32	91	35	573

from a given length; this is not a biologically reasonable model. Traditionally, length has been viewed as the independent variable that is measured with no error and weight as the random dependent variable that is measured with error. The validity of these assumptions is beyond the scope of this paper and will not be discussed. We have concerned ourselves with the appropriateness of two statistical models, the log-linear and nonlinear models. The log-linear model, with log-additive error, was written as

$$\ln W_i = \ln b_2 + a_2 \ln L_i + \ln \epsilon_{2i}. \tag{2}$$

The arithmetic equivalent of this model can be written as

$$W_i = b_2 L_i^{a_2} \epsilon_{2i},$$

but this equation should not be construed to be the model. The nonlinear model, with additive error, was written as

$$W_i = b_3 L_i^{a_3} + \epsilon_{3i}. \tag{3}$$

The evaluation of the goodness of fit of regression lines can be divided into distinct tests of precision (or significance) of the regression and of the appropriateness of the model. The appropriateness of a model (Equation 2 or 3) was tentatively accepted, and the model was fitted to the data. The precision of this fit can then be measured by the "*F*" test and the "*t*" test, both of which test H_N: $a = 0$ and H_A: $a \neq 0$, or the "R^2" statistic, the "proportion of total variation about the mean $\bar{Y}$ [$\bar{W}$] explained by regression" (Draper and Smith, 1966). All of these tests are equivalent and basically measure the usefulness of the regression as a predictor. To be able to perform any of these tests, the random error term must be normally distributed. The distribution of $\epsilon'_{2i} = \ln \epsilon_{2i}$ was tested for the log-linear model by calculating R.A. Fisher's statistics for skewness (G1) and kurtosis (G2, measuring the amount of peakness or bimodality). A model can fail in the significance tests because the model is incorrect or because the sample size is small relative to the amount of variability in the data. In addition, if a model is nonlinear in its parameters, it is not possible to test for significance because the variance estimates are biased, making it superfluous to test the distribution of the error term, ϵ_{3i}. Moreover, the residual sums of squares for linear and nonlinear least squares fitting routines cannot be compared because they are minimal estimates in their respective sample spaces. We chose to present the "R^2" and "*F*" statistics for the log-linear model as an indication of precision, but did not use the statistics in deciding best fit, since they cannot be compared to those obtained for the nonlinear model.

Our criteria for best fit of the models were based on measures of appropriateness, namely, whether the error terms have the following properties:

[4]
$$\begin{gathered} E[\epsilon'_{2i}] = 0 \text{ or } E[\epsilon_{3i}] = 0 \\ \mathrm{Var}(\epsilon'_{2i}) = \sigma_2^2 \text{ or } \mathrm{Var}(\epsilon_{3i}) = \sigma_3^2, \end{gathered} \tag{4}$$

that is, the error terms have a mean equal to zero and a constant variance. The error terms for the log-linear model must have a mean equal to zero, since an intercept term was included in the model (Draper and Smith, 1966, p. 87). For the nonlinear model, it is not readily apparent that the error term must be equal to zero; hence, the mean was calculated. The residuals were plotted against the dependent and independent variables to check for constant variance. If variance is constant, the residuals appear as a horizontal band along the variable axes (Draper and Smith, 1966, p. 86).

The final regression coefficients, or coefficients of allometry, were tested using the hypothesis scheme H_N: $a = 3.0$, H_A: $a \neq 3.0$ (Steel and Torrie, 1960, p. 171).

In reporting the results of the various statistical tests, the following convention was used: "NS" indicates not significant at the 0.05 level, "*, **, ***" indicate significance at the 0.05, 0.01, 0.001 levels, respectively; and "*d.f.*" stands for degrees of freedom.

RESULTS

Growth Stanzas

The weight-length data for each species were first plotted with logarithms of weight versus logarithms of fork length in order to subjectively check for more than one growth stanza (Tesch, 1968). Blue marlin

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[4] From this statement, the estimated value of the log-error term, ϵ'_{2i}, may be taken as zero which in turn indicates that $\hat{\epsilon}_{2i}$ in the arithmetic equivalent to the log-linear model (Equation 2) may be taken as equal to one. If the arithmetic equivalent to the log-linear model were designated as a separate model, it does not follow that $E\,[\epsilon_{2i}] = 1$ or that $\mathrm{Var}(\epsilon_{2i}) = \sigma_2{}^2$.

Table 2.—Weight-length relationships for billfishes using the log-linear model (Equation 2). The pooled category under the data set heading indicates pooling of longline and trolling data. Dashes indicate that statistical tests were not appropriate. The pooled data for blue marlin includes trolling-derived data for which sex was not determined.

Species	Data set	Sample size (*N*)	*b*	*a*	R^2 in percent	Variance			G1[1]	G2[1]	*F*[1]
						$\ln W.\ln L$	*a*	*b*			
Black marlin	Pooled	24	2.3787×10^{-6}	3.1654	97.2	0.0069	0.0131	0.4134	—	—	766.36***
Blue marlin 50-135 cm FL	Longline	4	5.1827×10^{-1}	0.6678	96.4	0.0072	0.0084	0.1654	—	—	52.93*
Blue marlin ≥135 cm FL	Pooled	[2]453	5.0048×10^{-6}	3.0214	95.0	0.0126	0.0326	0.0011	−0.29**	1.77**	—
	Longline	68	4.7226×10^{-6}	3.0442	96.2	0.0172	0.0055	0.1672	0.13 NS	—	1,677.27***
	Trolling	[2]385	5.0811×10^{-6}	3.0165	94.7	0.0116	0.0013	0.0406	−0.58**	2.09**	—
	Trolling	384	4.2968×10^{-6}	3.0470	94.9	0.0111	0.0013	0.0404	−0.48**	1.88**	—
	Trolling (male)	276	2.2929×10^{-5}	2.7405	82.7	0.0118	0.0057	0.1719	−0.72**	2.62*	—
	Trolling (female)	[2]86	3.9820×10^{-6}	3.0611	92.0	0.0153	0.0096	0.3171	−0.73**	1.95*	—
	Trolling (female)	85	1.9445×10^{-6}	3.1871	93.2	0.0127	0.0089	0.2914	−0.12 NS	−0.29 NS	1,144.57***
Sailfish	Pooled	18	2.0739×10^{-5}	2.6054	84.8	0.0228	0.0762	2.1770	—	—	89.04***
Shortbill spearfish	Pooled	16	5.0083×10^{-8}	3.8338	65.2	0.0332	0.5596	14.3795	—	—	26.27***
Striped marlin	Pooled	53	5.7126×10^{-7}	3.3756	93.1	0.0336	0.0166	0.4723	1.14**	—	—
Swordfish	Pooled	7	2.3296×10^{-7}	3.5305	98.9	0.0169	0.0286	0.8401	—	—	435.34***

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[1] *** indicates significance at the 0.001 level, ** indicates significance at the 0.01 level. NS indicates not significant at the 0.05 level. indicates significance at the 0.05 level.

[2] These data sets include the same single aberrant datum.

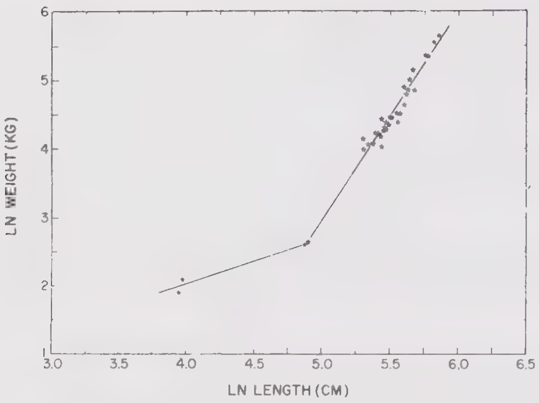

Figure 1.—Blue marlin data from longline data are plotted on a log-log scale to show the existence of two growth stanzas. The straight lines were fitted by eye.

was the only species exhibiting such a trend (Fig. 1) and then only for the longline-caught fish. Although it was quite evident that two growth stanzas existed, there were too few data to determine exactly where the two stanzas met or overlapped. We arbitrarily took the two data points at 135 cm FL (4.9 in natural logarithms) as the overlap area, with the assumption that the length-weight relationship for the older, well-represented stanza should be accurately predicted even if it actually began at a smaller size while that for the younger stanza is provisional. The younger growth stanza was treated separately in the subsequent analyses.

Log-Linear Model

The log-linear model (Equation 2) was fitted to the data for all species (Table 2). The "*F*" tests for black marlin, sailfish, shortbill spearfish, and swordfish were highly significant. Though the idea that a log-linear relationship between weight and fork length might not exist was rejected, this was a provisional conclusion because the validity of the statistical tests could not be checked. The proportion of the total variation accounted for by the regression, R^2, was high for all species except for the shortbill spearfish, where the usefulness of the relationship as a predictor was not great. For striped marlin, although the "R^2" value was high, the distribution of the error term was not normal. The sample size was too small to evaluate kurtosis, but since the more critical condition of skewness was highly significant, tests of significance could not be performed. For comparative purposes, the log-linear model was fitted to the pooled data for the blue marlin, and, as was the case for striped marlin, the error term was not normally distributed. For the blue marlin longline data, the error term was not skewed, and there were too few data to test for kurtosis. Tentatively accepting the error term as being normally distributed, the "*F*" test showed that the regression was highly significant. For the trolling data, the error term was not normally distributed; hence, tests of significance could not be performed. Examination of the error terms showed that there was one aberrant datum;

Table 3.—Weight-length relationships for blue and striped marlins using the nonlinear model (Equation 3). The data sets pooled category indicates pooling of longline and trolling data.

Species	Data set	Sample size (*N*)	*b*	*a*	R^2 in percent	$\bar{\epsilon}$	G1[1]	G2[1]
Blue marlin ≥135 cm FL	Pooled	453	6.3087×10^{-6}	2.9827	93.1	−0.5717	—	—
	Longline	68	3.9290×10^{-6}	3.0821	94.4	−1.1889	—	—
	Trolling	385	8.5300×10^{-6}	2.9265	92.2	−0.6549	−2.299**	36.691**
	Trolling	384	1.9421×10^{-6}	3.1895	98.9	0.3003	−0.266*	3.723**
	Trolling (male)	276	18.9972×10^{-6}	2.7756	83.1	0.1438	0.121 NS	2.894**
	Trolling (female)	86	4.8246×10^{-6}	3.0249	90.8	0.4055	−2.991**	20.499**
	Trolling	85	1.7082×10^{-6}	3.2111	91.9	−0.1341	−0.067 NS	0.577 NS
Striped marlin	Pooled	53	1.0978×10^{-6}	3.2589	90.7	−0.1553	—	—

[1] ** indicates significance at the 0.01 level, * indicates significance at the 0.05 level, and NS indicates not significant at the 0.05 level.

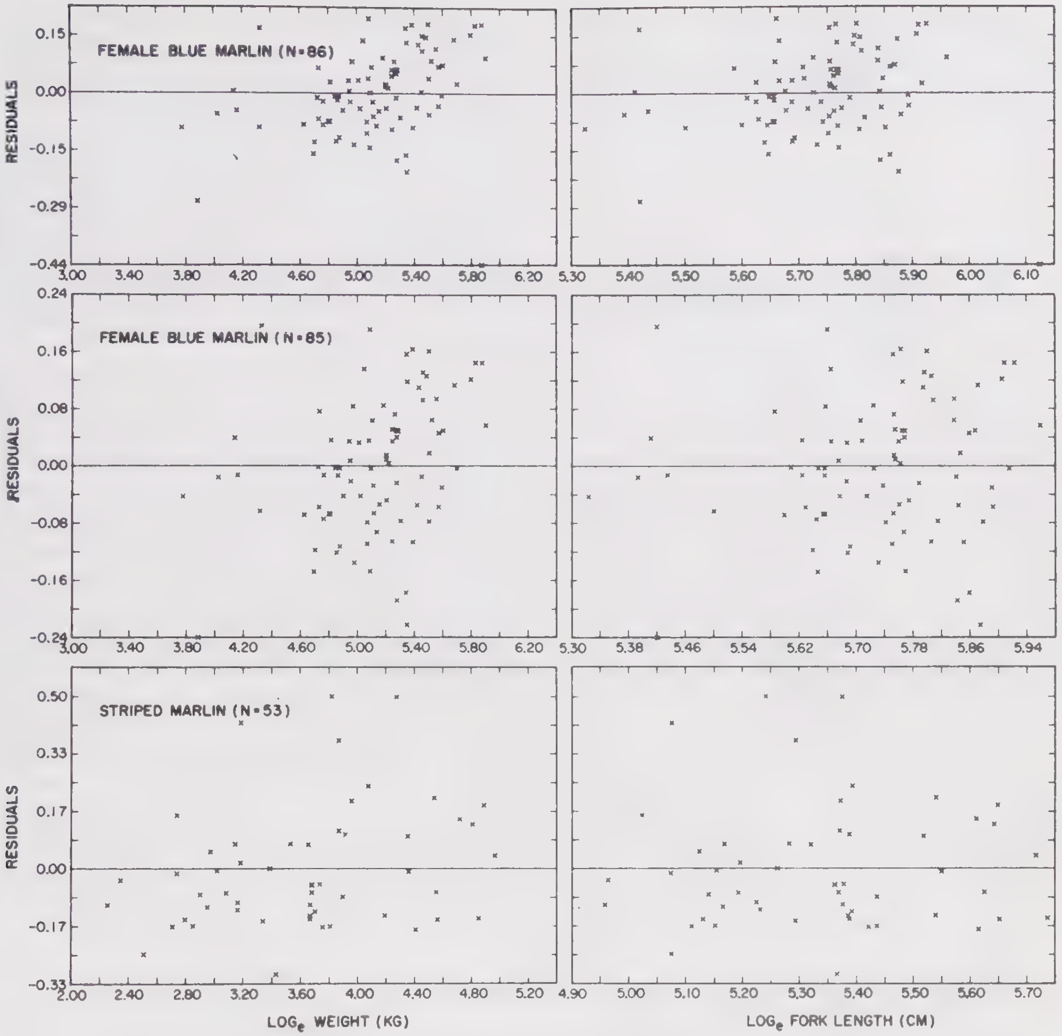

Figure 2.—Plot of residuals from the log-linear model for female blue marlin with 86 and 85 samples and for striped marlin with 53 samples. Weight was recorded in kilograms and fork length in centimeters.

however, the elimination of this datum did not alter the results significantly. When the trolling data were divided into males and females, the error terms were still not normally distributed. However, when the above mentioned aberrant datum for the female data was dropped from the calculations, the error terms were normally distributed. The "*F*" test showed that the relationship was highly significant, and the relationship accounted for 93% of the variation in the data.

For large blue marlin (five relationships) and striped marlin, the residuals about the regression line were plotted against the dependent (weight) and independent (fork length) variables in order to evaluate the fit of the log-linear model. In every case, the distribution of the residuals appeared as a band along the axes; hence, the model appeared to fit the data. The results for striped marlin and blue marlin (trolling data for females with all data points and with the one aberrant datum point dropped) were representative of all the species plots. These results are presented in Figure 2. The two plots for the blue marlin indicated the effect of the aberrant datum that was discussed earlier when the normality of the residuals was tested. In spite of the residuals not being normally distributed for all except two of

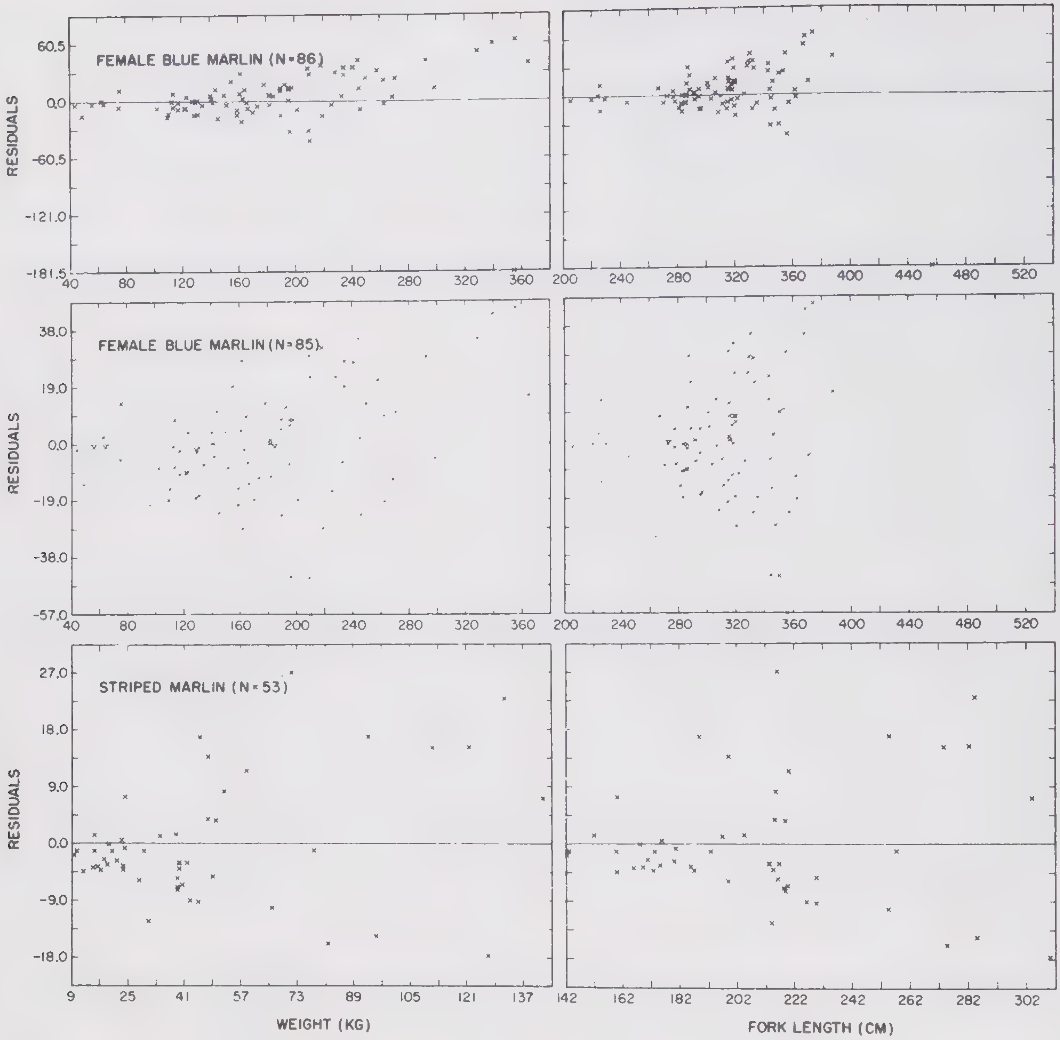

Figure 3.—Plot of residuals from the nonlinear model for female blue marlin with 86 and 85 samples and for striped marlin with 53 samples.

the cases (Table 2), the plotting of the residuals indicated that there was no reason to reject the assumption of constant variance. Hence, the log-linear model seemed to be appropriate.

Nonlinear Model

The nonlinear model (Equation 3) was fitted to the data for the large blue marlin (five relationships) and the striped marlin (Table 3) in order to compare the fit of this model to that for the log-linear model. Since the estimate of σ^2 is biased in nonlinear regression and therefore tests of significance cannot be made, the distribution of the error terms was not tested. The estimates of "R^2" (a biased estimator in this nonlinear case) indicated that the nonlinear model does not in general account for as much of the variation in the data and is, therefore, not as good a predictor as the log-linear model. When the residuals from the nonlinear regression lines were plotted against the dependent and independent variables, it was found in every case that the amount of error was small for small values of the variables and large for large values of the variables. Hence, the assumption of constant variance of the error term must be rejected for all cases. The results for blue marlin, trolling data for females with 86 and 85 data points, and for striped marlin presented in Figure 3 were representative of all species plots. Comparing these plots with those in Figure 2 showed that the nonlinear model did not fit the data as well as did the log-linear model. Since both assumptions regarding the properties of the error terms were rejected, it must be concluded that the nonlinear model is not appropriate for these sets of data.

Coefficients of Allometry

The coefficients of allometry that will be discussed in this section were obtained from the fitting of the log-linear model. For those species and data sets in Table 2 where the assumption of normality of the residuals was rejected, the coefficients of allometry were not tested. The hypotheses tested were H_N: $a = 3.0$ and H_A: $a \neq 3.0$ (a two-sided "*t*" test), and the results of these tests are presented in Table 4. For small blue marlin and swordfish, the null hypothesis that $a = 3.0$ was rejected on the basis of the data available. For black marlin, large blue marlin (longline data), female blue marlin, sailfish, and shortbill spearfish, the alternate hypothesis that $a \neq 3.0$ was rejected on the basis of the data available.

DISCUSSION

Weight-length relationships were fitted successfully for all six species of billfishes appearing in the Honolulu Laboratory's collections (Figs. 4 and 5). The log-linear relationships (Table 2) were found to be more appropriate than the nonlinear relationships (Table 3) for every species and data set. The significance of all the relationships was not testable since many of the error terms were not normally distributed; however, the "R^2" values indicated that all of the relationships, except for the shortbill spearfish, account for a high percentage of the variance in the data. Hence, on the basis of fit and amount of variance accounted for, these relationships should be good predictors.

However, the usefulness of the relationships as predictors also varies according to the amount of

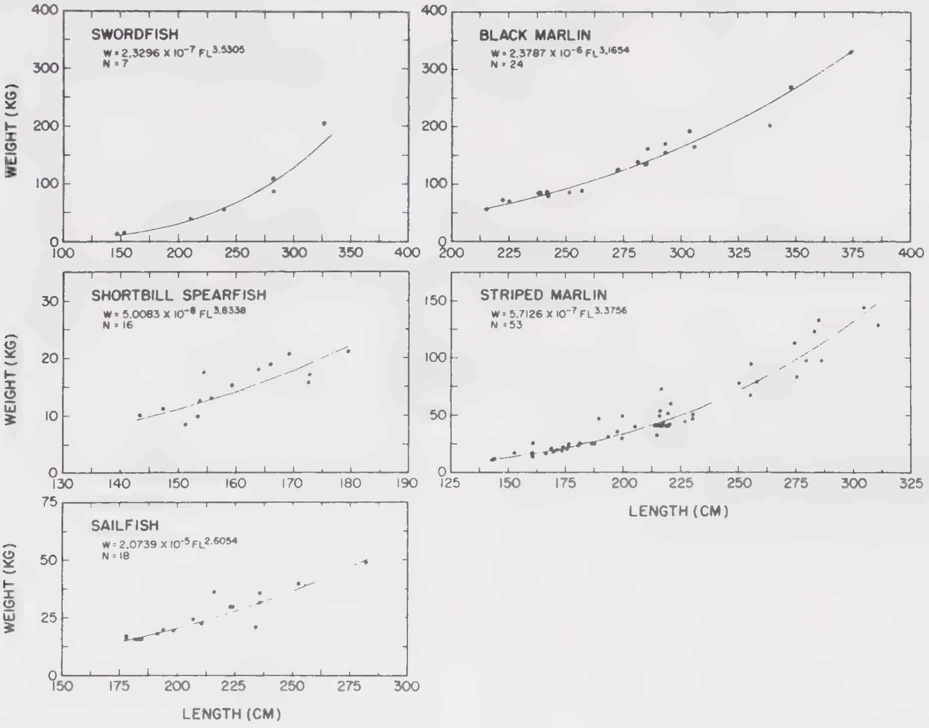

Figure 4.—Weight-length relationships using the log-linear model for swordfish, shortbill spearfish, sailfish, black marlin, and striped marlin.

Table 4.—Final weight-length relationships using the log-linear model, $W = bL^a\epsilon$, for the indicated data sets. H_N indicates the null hypothesis tested, and the accompanying alternate hypothesis was then $H_A: a \neq 3.0$. The data for the eastern tropical Pacific were obtained from Kume and Joseph (1969). Dashes indicate that the test could not validly be performed. Size ranges are in centimeters fork length.

Species	Data set	Sample size (*N*)	*b*	*a*	[1]*t* for $H_N: a = 3.0$	Size range	Eastern Tropical Pacific *b*	Eastern Tropical Pacific *a*	Eastern Tropical Pacific Size range
Black marlin	Pooled	24	2.3787×10^{-6}	3.1654	1.447 NS	214.5-373.0	—	—	—
Blue marlin 50-135 cm FL	Longline	4	5.1827×10^{-1}	0.6678	−25.410**	50.0-135.0	—	—	—
Blue marlin ≥135 cm FL	Pooled	453	5.0048×10^{-6}	3.0214	—	135.0-456.9	—	—	—
	Longline	68	4.7226×10^{-6}	3.0442	0.595 NS	135.0-401.2	3.585×10^{5}	2.822	167.0-270.0
	Trolling	384	4.2968×10^{-6}	3.0470	—	156.0-389.2	—	—	—
	Trolling (male)	276	2.2929×10^{-5}	2.7405	—	176.5-311.0	—	—	—
	Trolling (female)	85	1.9445×10^{-6}	3.1871	1.986 NS	205.2-387.2	—	—	—
Sailfish	Pooled	18	2.0739×10^{-5}	2.6054	− 1.429 NS	177.0-281.0	1.1596×10^{4}	2.461	134.0-205.0
Shortbill spearfish	Pooled	16	5.0083×10^{-8}	3.8338	1.115 NS	140.0-180.0	1.5320×10^{7}	3.724	128.0-156.0
Striped marlin	Pooled	53	5.7126×10^{-7}	3.3756	—	142.2-310.1	5.5564×10^{6}	3.089	108.0-211.0
Swordfish	Pooled	7	2.3296×10^{-7}	3.5305	3.135*	145.2-324.5	2.1115×10^{5}	2.961	131.0-229.0

[1] ** indicates significance at the 0.01 level, * indicates significance at the 0.05 level, and NS indicates not significant at the 0.05 level.

data used in the analysis, the range of the data, and whether sexes were analyzed separately. Considering the sample size (4) and the method of selecting the points of overlap, the relationship for small blue marlin (50-135 cm FL) was provisional. The relationship for shortbill spearfish was also provisional since there were 16 data points ranging from 140.0 to 180.0 cm FL. Although the sample sizes for black marlin, sailfish, and swordfish were small (24, 18, and 7, respectively), the ranges were wide, and the relationships should be taken as valid estimates. For striped marlin and for blue marlin, considering all data sets, there were enough data to obtain valid relationships. The importance of the results for the various blue marlin data sets will be discussed in connection with the coefficients of allometry.

Concrete interpretations of the coefficients of allometry are precluded by a statistical inability to test the significance of all the coefficients as well as to test between coefficients of different species or data sets. The coefficient for swordfish was the only one tested that was apparently greater than 3.0. For the other species tested, black marlin, blue marlin (longline data), female blue marlin (trolling data), sailfish, and shortbill spearfish, the hypothesis that the coefficient was equal to 3.0 could not be rejected. That is, the growth in weight to length was isometric for these species. Intuitively, we doubt these results for sailfish and shortbill spearfish and suspect that additional data would show the coefficient for sailfish to be less than isometry and for shortbill spearfish to be greater than isometry.

For blue marlin, the interpretation of the results was complicated by an inability to perform statistical tests of hypotheses. The coefficient of allometry for the small blue marlin indicated that the small fish maintain a very different weight to length growth relationship than do the larger, adult fish. Part of this difference may have been due to differential growth of the bill in the younger fish. It was apparent from Table 4 that there was not a real difference between longline- and troll-caught blue marlin; the coefficients of allometry as well as the intercept "*b*" were extremely similar. This does not necessarily imply that there are no seasonal differences in the weight-length relationship of blue marlin but does indicate that no such effect could be shown with 68 data points from longline catches made over all seasons. When the trolling data were divided according to sex, it was found that the coefficient for females did not differ significantly from isometry while that for males was probably less than isometry. The male and female curves (Fig. 5) could not be distinguished where the data overlapped. Hence, the increased weight to length growth shown by the females occurs primarily at lengths greater than those attained by males in this

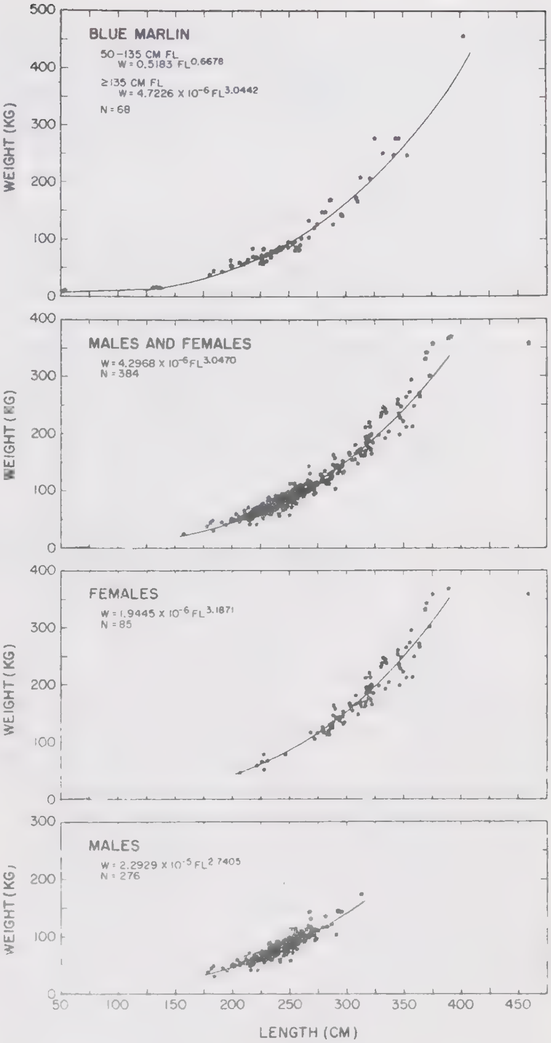

Figure 5.—Weight-length relationships using the log-linear model for blue marlin. The upper chart represents the relationships found for small and large fish using longline data. The remaining three charts represent relationships for sexes combined (including sex undetermined), females, and males using trolling data. The aberrant datum appearing in the sexes combined and female charts for the trolling data was not used in the calculation of the relationships.

data set. The sexual dimorphism in length that has been noted by many workers (e.g., Strasburg, 1970) apparently extends to the weight-length relationship also. That is, females not only grow to a greater length than males, but are proportionally heavier at the same length.

For striped marlin, analysis of the pooled data produced an estimate of the coefficient of allometry that appears to be greater than isometry. Inability to divide the data by sex was unfortunate since it is not known whether sexually dimorphic growth characteristics exist for the striped marlin. If such an effect does exist, it is believed to be less marked than in the blue marlin. Hence, the largeness of the striped marlin coefficient relative to that for the blue marlin, for both pooled and female data alone, probably was not due to sexual dimorphism.

There are only two papers in the literature giving weight-length relationships that may be compared to ours, since the data used by Royce (1957) were included in this analysis. De Sylva (1957) presented a length-weight plot for sailfish from the Atlantic Ocean, but a model was not fitted to the data. A fish approximately 250 cm FL would weigh 34 kg whereas our study predicts 37 kg. Kume and Joseph (1969) fitted the log-linear model to blue marlin, sailfish, shortbill spearfish, striped marlin, and swordfish data. The coefficients of allometry and the intercept points from their calculations are presented in Table 4 for direct comparison to those from this study. For all species, the coefficients of allometry for fish from the central Pacific were greater than those from the eastern tropical Pacific. If the coefficients were shown to be statistically different, there would be little point in comparing the intercept values since the relationships would already have been shown to be different. However, since the intercept value is related to the coefficient of condition, it should be noted that all of the intercept values for the central Pacific fish were smaller than those for the eastern tropical Pacific fish by a factor of 10. These differences may not be real because the samples for the central Pacific contained larger individuals than did the samples for the eastern tropical Pacific.

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7439

Angler Catch Rates of Billfishes in the Pacific Ocean

JAMES L. SQUIRE, JR.[1]

ABSTRACT

In 1969, 1970, and 1971 marine game fish anglers participating in the Pacific phase of the National Marine Fisheries Service cooperative marine game fish tagging program were asked to complete a postcard form which requested information of the number of days of billfishing the angler engaged in and the catches made. From the 17,876 angler days reported, the catch consisted of 10,234 billfishes. The average for the 3-yr period was 0.57 billfish per angler-day or 1.75 days of fishing per billfish. Analysis of data for the geographical areas in the eastern Pacific and Australia (Queensland) where billfishing is conducted resulted in a wide range of catch per effort for all billfish species combined. Off southern California, U.S.A., the catch was 0.10 fish per angler-day, equaling 10.3 days of fishing per fish. Off Baja California, Mexico, records show 0.82 fish per angler-day equaling 1.22 days fishing per fish, and fishing off Mazatlán yielded 1.21 fish per angler-day and 0.82 days fishing per fish. Off Acapulco, Mexico, the results were 0.95 fish per angler-day and 1.05 days per fish. Fishing off Australia the records show 0.55 fish per angler-day equaling 1.83 days per fish.

The measurement of catch rates is of value in evaluating fishing success relative to seasonal changes, specific types of fishing gear or changes in gear, and effects of environmental change. However, its greatest use has been in the determination of the effect of fishing on the stock or stocks of fish being utilized by sport and commercial fisheries.

The only comprehensive sources of catch and effort data for billfishes in the Pacific Ocean are the reports of the commercial longline fishery for tunas and billfishes published by the Research Division of the Japanese Fisheries Agency. These data have been used by researchers in the eastern Pacific in determination of commercial catch rates for billfishes (Suda and Schaefer, 1965; Kume and Schaefer, 1966; Kume and Joseph, 1969).

The billfish sport fishery in the northeastern Pacific off Mexico and the United States is reported to capture at least 10,000 fish each year (Talbot[2]); however no accurate totals for sport-caught billfishes are available. The number of billfishes taken by the sport fishery is a fraction of that landed by the commercial fishery. However, the economic value of the sport fishery resulting from the expenditure for goods and services by the thousands of billfish anglers in the pursuit of the sport is assumed to be substantial.

The problems in obtaining a measure of catch and effort in marine sport fisheries are many. In contrast to a commercial fishery, where commercial landings and sometimes fishing records are kept and the number of operating units is known, the sport fishery consists of many small and mobile units which may or may not land their billfishes at locations where a record of the landing might be made. A report on the problem of obtaining sport fishery statistics was made by the Institute of Statistics, University of North Carolina (D. W. Hayne, 1964[3]) and many of the observations in that report are applicable to the design of a statistically accurate billfish angler survey.

As part of the cooperative marine game fish tagging program, conducted first at the Tiburon Marine Laboratory, Tiburon, California, and later at the Southwest Fisheries Center, La Joila, California, an annual report describing the progress in billfish tag-

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 90237.

[2] Talbot, Gerald B., U.S. Bureau of Sport Fisheries and Wildlife, Clemson University, P.O. Box 429, Clemson, S.C. Personal communication.

[3] Hayne, D. W., The measurement of catch and effort in marine sportfishing. Report to the U.S. Bureau of Sport Fisheries and Wildlife, September 15, 1964. Institute of Statistics, Raleigh Section, North Carolina State, University of North Carolina, memo, 23 p.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972
Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.

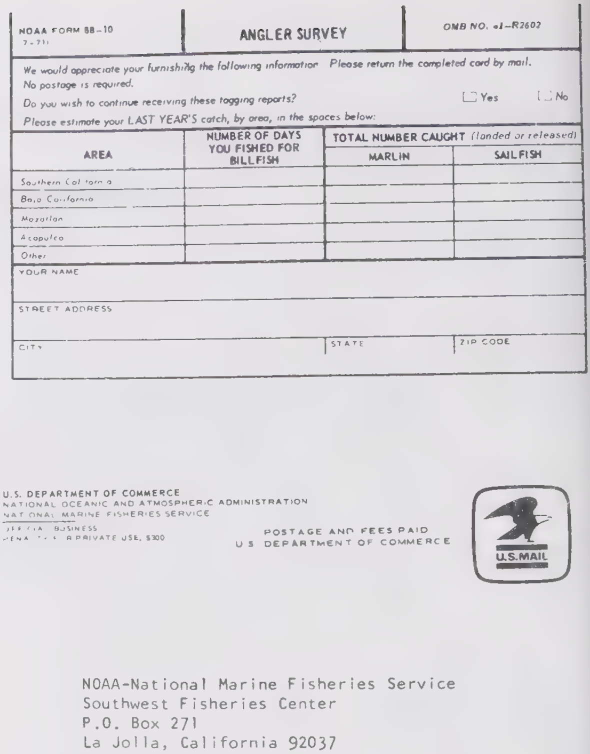
ging was mailed to individuals that had participated in the program. This mailing list consisted of names of billfish anglers, most of whom fished in the eastern Pacific or off the east coast of Australia.

In the annual reports for 1969, 1970, and 1971, a postcard was enclosed requesting information on the amount of fishing effort and catch. The billfish angler was asked to recall the number of days of billfishing and the number of billfish caught by species. The anglers were requested to give an "honest" answer and told that information on zero catches was important. The technique of postcard survey has been the subject of considerable controversy. The California Department of Fish and Game has used this technique and a number of researchers have published on the results of this type of survey (Calhoun, 1950, 1951; Clark, 1953; Pelgen, 1955; Abramson, 1963; Jensen, 1964).

Hayne reported that it is difficult for a fisherman to remember precisely his catch of the previous year. However, with regard to billfishes, the frequency at which the average billfish angler participates in the sport is limited and the annual catch of billfish per angler is small. Billfish are "trophy fish" and the author believes that the average billfish angler can recall within close limits the number of fish caught during the previous year and the number of days he participated in the fishery.

METHODS

A sample of the questionnaire used is shown in Figure 1. The form was also used to update the mailing list for the Cooperative Marine Game Fish Tagging Program annual report. The postcard form was sent to the billfish anglers in February of 1970, 1971, and 1972, and a prompt return of the card was requested. The number of survey cards sent each



NOAA FORM 88–10
7-71

ANGLER SURVEY

OMB NO. 41–R2602

We would appreciate your furnishing the following information Please return the completed card by mail. No postage is required.

Do you wish to continue receiving these tagging reports? ☐ Yes ☐ No

Please estimate your LAST YEAR'S catch, by area, in the spaces below:

AREA	NUMBER OF DAYS YOU FISHED FOR BILLFISH	TOTAL NUMBER CAUGHT *(landed or released)*	
		MARLIN	SAILFISH
Southern California			
Baja California			
Mazatlan			
Acapulco			
Other			

YOUR NAME

STREET ADDRESS

CITY | STATE | ZIP CODE

U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL MARINE FISHERIES SERVICE
OFFICIAL BUSINESS
PENALTY FOR PRIVATE USE, $300

POSTAGE AND FEES PAID
U S DEPARTMENT OF COMMERCE

U.S.MAIL

NOAA-National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92037

Figure 1.—Angler survey card.

Table 1.—Combined catch and effort data for surveys conducted in 1969, 1970, and 1971.

Area	Angler days	Species/catch (numbers)			Catch rates	
		Striped marlin	Sailfish	Black marlin	Fish/angler day	Days/fish
USA						
Southern California	6,458	593	51	0	0.10	10.03
Mexico						
Baja California	8,710	6,168	964	0	0.82	1.22
Mazatlán	1,316	697	900	0	1.21	0.82
Acapulco	249	16	221	0	0.95	1.05
Australia (Queensland)						
Cairns	1,143	0	172	452	0.55	1.83
Total	17,876	=10,234 (all species)			Aver. 0.57	Aver. 1.75

year with the annual tagging report varied from 1,900 to 2,600.

RESULTS

Approximately 50% of the survey cards were returned within a 3-mo period and the number of angler days in each of the major fishing areas, the number of billfishes caught, and calculations of numbers of fish per angler day and numbers of days of fishing per fish are given in Table 1.

The combined totals for the fishing areas off southern California, U.S.A., about the tip of Baja California, Mazatlán, and Acapulco, Mexico, and Cairns, Queensland, Australia, were 17,876 angler days, catching 10,234 billfishes for an average of 0.57 fish per day and 1.75 days of fishing for each billfish.

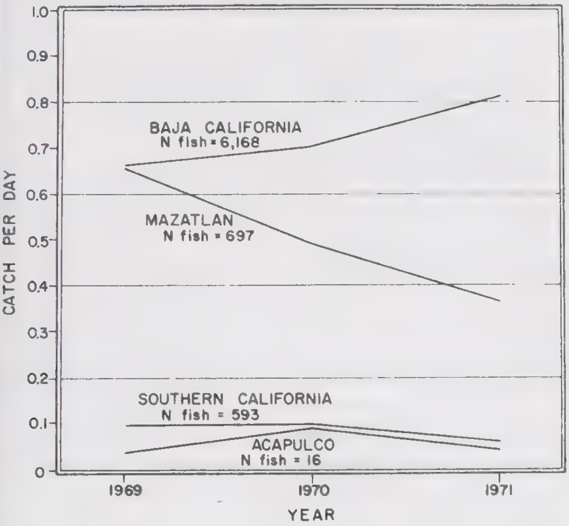


Figure 2.—Sport fishing catch per day for striped marlin in the eastern Pacific.

A breakdown of the totals given in Table 1 for each year is presented in Table 2.

For these selected fishing areas the annual statistics from the survey on total catch and effort are as follows: 1969, 6,286 angler days, 3,404 billfishes caught equaling 0.54 fish per day and 1.90 days of fishing per fish; 1970, 6,286 angler days, 3,588 billfishes caught equaling 0.58 fish per day and 1.75 days of fishing per fish; 1971, 5,304 angler days, 3,242 billfishes caught equaling 0.61 fish per day and 1.64 days of fishing per fish.

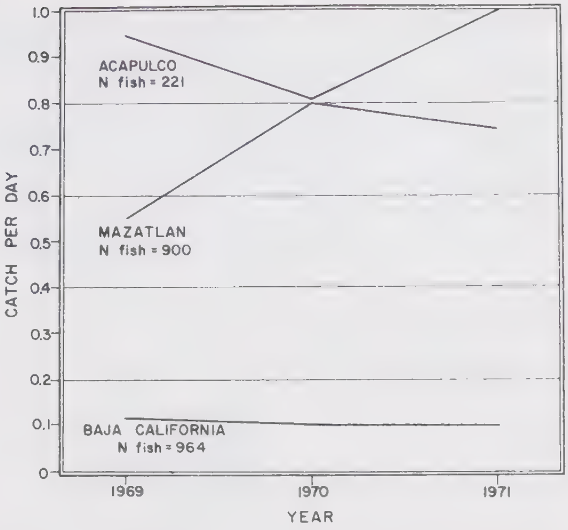


Figure 3.—Sport fishing catch per day for sailfish in the eastern Pacific.

A graphic presentation of the catch per effort data is given for striped marlin *Tetrapturus audax* in Figure 2; for sailfish *Istiophorus platypterus* in Figure 3; and for black marlin *Makaira indica* in Figure 4. Catch per effort data for combined

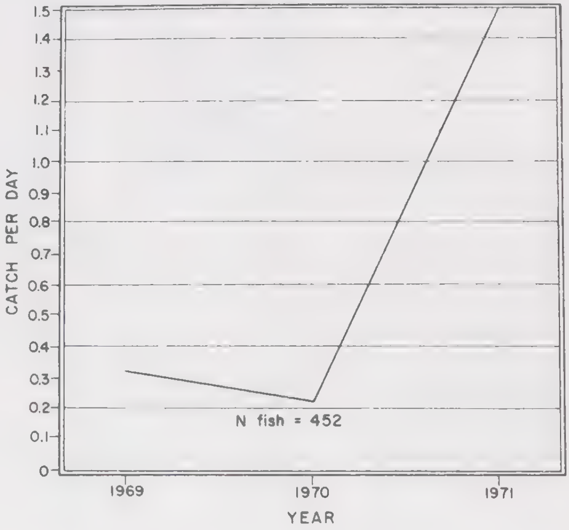


Figure 4.—Sport fishing catch per day for black marlin off Queensland, Australia.

Table 2.—Catch and effort data for the years 1969, 1970, and 1971 by species and by area.

Area	Angler days	Striped marlin			Sailfish			Black marlin			Total		
		Catch	Catch/ angler day	Days/ fish	Catch	Catch/ angler day	Days/ fish	Catch	Catch/ angler day	Days/ fish	Catch	Catch/ angler day	Days/ fish
1969													
Southern California	2,297	220	0.10	10.44	—	—	—	—	—	—	220	0.10	10.44
Baja California	2,519	1,657	0.66	1.52	314	0.12	8.02	—	—	—	1,971	0.78	1.27
Mazatlán	583	382	0.65	1.52	322	0.55	1.81	—	—	—	704	1.21	0.83
Acapulco	112	5	0.04	10.70	106	0.94	1.05	—	—	—	111	0.94	1.05
Cairns (Australia)	775	—	—	—	162	0.21	4.66	236	0.31	3.20	398	0.53	1.93
1970													
Southern California	2,068	221	0.01	9.30	11	<0.00	88.0	—	—	—	232	0.11	8.90
Baja California	3,398	2,258	0.70	1.50	357	0.10	9.50	—	—	—	2,615	0.77	1.30
Mazatlán	461	214	0.50	2.10	374	0.80	1.20	—	—	—	588	1.27	0.80
Acapulco	97	9	0.09	10.70	75	0.80	1.20	—	—	—	84	0.86	1.15
Cairns (Australia)	262	—	—	—	10	0.03	26.2	59	0.22	4.40	69	0.26	3.70
1971													
Southern California	2,093	152	0.07	13.70	40	0.02	52.30	—	—	—	192	0.09	10.90
Baja California	2,793	2,253	0.82	1.24	293	0.10	9.50	—	—	—	2,546	0.91	1.10
Mazatlán	272	101	0.37	2.69	204	0.75	1.33	—	—	—	305	1.12	0.89
Acapulco	40	2	0.05	20.00	40	1.00	1.00	—	—	—	42	1.05	0.95
Cairns (Australia)	106	—	—	—	—	—	—	157	1.48	0.69	157	1.48	0.69

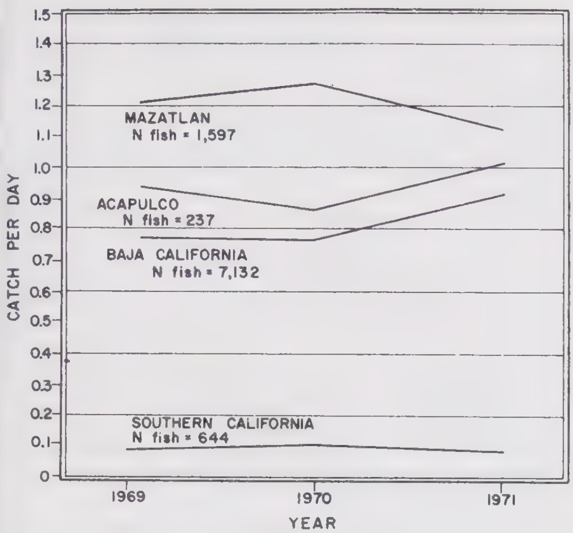


Figure 5.—Combined species (striped marlin and sailfish) catch per day in the eastern Pacific.

species of billfish at locations in the eastern Pacific are shown in Figure 5.

SUMMARY AND DISCUSSION

Striped marlin catch and effort data for fishing off southern California show a catch rate of 0.10 fish per day or less, and the catch rate off Acapulco is lower than southern California. The Baja California, Mexico, catch rate is highest, ranging between 0.66 and 0.82 fish per day with a slight increase shown in the catch rate in 1971 as compared to 1969. For the fishing area off Mazatlán the catch rate has declined from 0.65 to 0.37 during the survey years.

During the 3-yr period catch rates for sailfish ranged about the 0.9 to 1.0 fish-per-day level off Acapulco and the 0.55 to 0.80 fish-per-day level off Mazatlán. The catch rate is much lower off Baja California than off Mazatlán and Acapulco, remaining steady at a rate of about 0.1 fish per day. Black marlin catch rates off Cairns, Australia varied considerably from a low of 0.22 to a high in 1971 of 1.48 fish per day.

In 1968 and 1969 the Tiburon Marine Laboratory conducted field sampling for billfishes about the tip of Baja California and at Mazatlán, Mexico. Catch and effort data were collected from available sources such as the sportfishing fleet operators and Mexico's Department of Tourism. Catch and effort data for Mazatlán and Las Palmas Bay (at the tip of Baja California) are shown in Figure 6. Statistical data from the field sampling program show a catch rate for sailfish at Mazatlán of 0.74 fish per day and the postcard angler survey shows about 0.70 fish per day. For striped marlin caught about the tip of Baja California, Mexico, the Las Palmas Bay data shows a catch rate of 0.60 fish per day, the angler postcard survey shows about 0.75 fish per day.

Comparative catch-per-unit-effort data are not available for southern California waters, but experienced anglers state the figure of 0.10 billfish per day appears reasonable.

Marine game fishing for billfishes is an important economic factor in many areas of the world. The monetary expenditure of marine anglers per billfish caught is recognized as substantial. The point

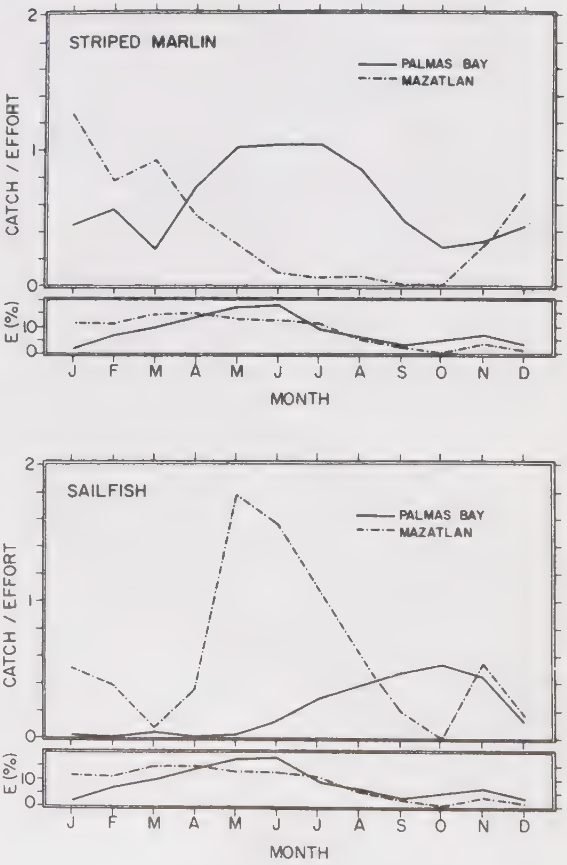


Figure 6.—Striped marlin (upper panel) and sailfish (lower panel) catch and effort rates off Las Palmas Bay (tip of Baja California) and Mazatlán, Mexico, 1968-1969.

(catch per effort level) at which the majority of anglers will cease to fish is dependent upon location and accessibility of the fishing grounds. An example of this is billfishing off southern California, which has by the angler survey records a low catch rate of 0.10 fish per day, or 10.02 days per billfish. The accessibility of the fishing grounds to the large southern California fleet of sportfishing boats makes for a large effort in spite of a low catch. If this same catch rate were common about the tip of Baja California, Mexico, the number of U.S. anglers traveling to this distant area to fish for billfishes might be only a fraction of the present number.

The angler survey sampled to a greater degree those individuals who participated in the tagging program, and had fished off southern California, the west coast of Mexico, west coast of Central America, or Australia. The postcard survey method for obtaining billfish catch and effort data has the potential of sampling more billfish anglers than any other method. Selection of a mailing list based on active billfish anglers belonging to the major billfish clubs throughout the United States and in other countries could provide a sampling frame for a reliable worldwide statistical determination of sportfishing catch and effort activity. The postcard method could provide a source of continuing information on the status of billfish angling relative to the resource base on which it depends for the least monetary expenditure, when compared with other sampling methods.

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7440

Catch Distribution and Related Sea Surface Temperature For Striped Marlin *(Tetrapturus audax)* Caught off San Diego, California

JAMES L. SQUIRE, JR.[1]

ABSTRACT

Records for 4,535 marlin landed at San Diego, California, and related sea surface temperature data were examined for the period 1963 through 1970 to determine time-space distribution and the relationship of catch and sea surface temperatures. For the period 1963 through 1970 the catch of 4,535 marlin was compared to sea surface temperature conditions relative to increased catches.

Catch distribution based on 1963 to 1967 data showed that 76.4% were caught within a 35- by 40-nautical-mile area off San Diego, with the maximum catch being made from mid-August to mid-September. Catch temperatures off southern California calculated for this area from airborne infrared sea surface temperature survey data ranged from 61° F (16.1°C) to 73° F (22.8°C); the mean catch temperature was 67.8° F (19.9°C).

Sea surface temperature conditions based on 2-week average temperature charts issued by the National Marine Fisheries Service indicate that an initial warming of water to an average temperature of 68° F (20.0°C) or above is related to an increase in catch. When average temperatures were below 68° F (20.0°C), 931 fish were caught; between 68° (20.0°C) and 70° F (21.1°C) the catch was 1,886 fish; and a further increase to 70° F (21.1°C) or above resulted in a catch of 1,718 fish.

Catch data and isotherm charts, 1963 through 1970, indicate that the continuity of the 68° F (20.0°C) and 70° F (21.1°C) isotherms from off central Baja California to off southern California is associated with improved fishing. When these isotherms were discontinuous the average catch per biweekly period was 82.0 fish; when these isotherms were continuous the average catch was 146.1 fish. The highest average catch per biweekly period (205.3 fish) was recorded when the 70° F (21.1°C) isotherm was continuous.

The striped marlin *(Tetrapturus audax)* is the object of a sport fishery in southern California waters during late summer and early fall. Sport fishing for striped marlin in these waters has been conducted since about 1903 (Howard and Ueyanagi, 1965) and striped marlin were caught commercially up to 1937. Since 1937 it has been illegal to land the species commercially in California. The early sport and commercial fishery was centered near Catalina Island and between the island and the mainland. In recent times the area off San Diego has experienced increased angling effort, and presently this area yields the largest number of sportcaught striped marlin. Most of the marlin are landed at three points in southern California: the Avalon Tuna Club, Avalon, Catalina Island; the Balboa Angling Club, Newport Beach; and the San Diego Marlin Club, San Diego. At these clubs each fish is weighed and information is recorded on a weight slip (Fig. 1).

Changes in sea surface temperature affect the distribution of many pelagic marine fishes commonly caught off southern California. During periods of high temperatures, greater numbers of the more important marine game species, such as Pacific bonito *(Sarda chiliensis)*, yellowtail *(Seriola dorsalis)*, and Pacific barracuda *(Sphyraena argentea)*, which are common to the lower west coast of Baja California, Mexico, migrate northward into higher latitides (Hubbs, 1916, 1948; Walford, 1931). Fishing success for albacore *(Thunnus alalunga)* off this area has been related to changes in sea surface temperature (Hester, 1961; Clemens and Craig, 1965). Radovich (1961, 1963) has also described the effects

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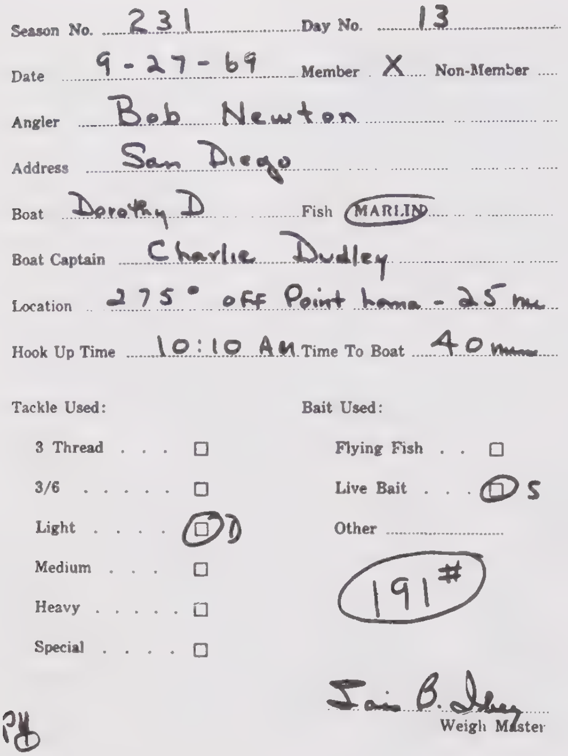
[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory, NOAA, La Jolla, CA 92037.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.



Season No. 231 Day No. 13

Date 9-27-69 Member X Non-Member

Angler Bob Newton

Address San Diego

Boat Dorothy D Fish [✓ MARLIN]

Boat Captain Charlie Dudley

Location 275° off Point Loma - 25 mi

Hook Up Time 10:10 AM Time To Boat 40 min

Tackle Used:

3 Thread . . . ☐

3/6 . . . . . . ☐

Light . . . . [✓ ☐] D

Medium . . . ☐

Heavy . . . . . . ☐

Special . . . . ☐

Bait Used:

Flying Fish . . ☐

Live Bait . . . [✓ ☐] S

Other

191#

Weigh Master

PH

Figure 1.—Weight slip used by the San Diego Marlin Club, San Diego, California.

of water temperature on the distribution of scombrid fishes common to the water off southern California and Baja California.

There are many physical and biological factors that can affect the distribution of fishes. Temperature, salinity, turbidity, and food supply (plankton and forage species) are but a few of these factors. However, knowledge of the precise degree to which one or a combination of factors affect distribution is not known. Temperature as one of the easily measured factors has been shown in some instances to affect distribution of organisms.

Observations of sea surface temperature prior to and immediately after the start of good fishing might give us some clues as to thermal conditions that may be contributing to successful striped marlin fishing. In this paper the temporal and geographical distribution of striped marlin catches off San Diego from 1963 to 1967 are described, and the relation of surface water temperature to fishing success during the period 1963 to 1970 is examined.

Since more striped marlin were landed at the San Diego Marlin Club than at any other location, I used their catch records to determine the geographical distribution of the catch for each month of the fishing season. These records provided catch location for 3,923 fish, but the fishing effort expended in catching this amount of fish is not known. These catch distribution data and sea surface temperature data derived from airborne temperature surveys were used in the calculation of the average or mean catch temperature off San Diego for all striped marlin caught during the major months of fishing for the years 1963 through 1967.

The cooperation of the San Diego Marlin Club in allowing use of its catch records is appreciated.

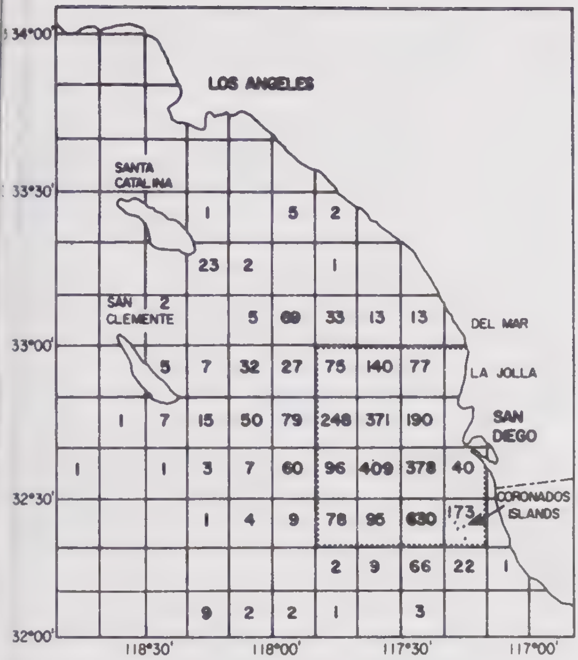
CATCH DISTRIBUTION

The temporal catch distribution for the 1963 to 1967 period is shown in Table 1. Catch records indicate that August, September, and October are the months having the major catches of striped marlin. Few are caught in July, and usually the November catch is minor. Most fish are caught between mid-August and mid-October, with fishing during the first half of September yielding more catch than any other half-month period. Peak annual catches were recorded for every biweekly period, 16-31 August through 1-15 October, for the years 1963 to 1967.

Table 1.—Striped marlin catch landed at the San Diego Marlin Club during half-month periods, July-November, 1963-1967

Month	1st half	2nd half	Monthly total
July	0	31	31
August	163	841	1,004
September	1,279	612	1,891
October	450	250	700
November	297	0	297
		Total	3,923

For the months of August, September, and October, catch locations of striped marlin were plotted on a chart divided into block areas of 10-minute latitude by longitude dimension. These areas are identical to the block area system used by the California Department of Fish and Game for determining catch locations for commercial and party boat catches (Young, 1963). The total catch over the 5-yr period by block area is shown in Figure 2, and the catch for each month is shown in Figures 3-5. Figure 2 shows that the major fishing area off San Diego outlined by a dark border can be described as being within the boundaries of lat. 32°20′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DEL MAR
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SAN DIEGO
CORONADOS ISLANDS
1 5 2
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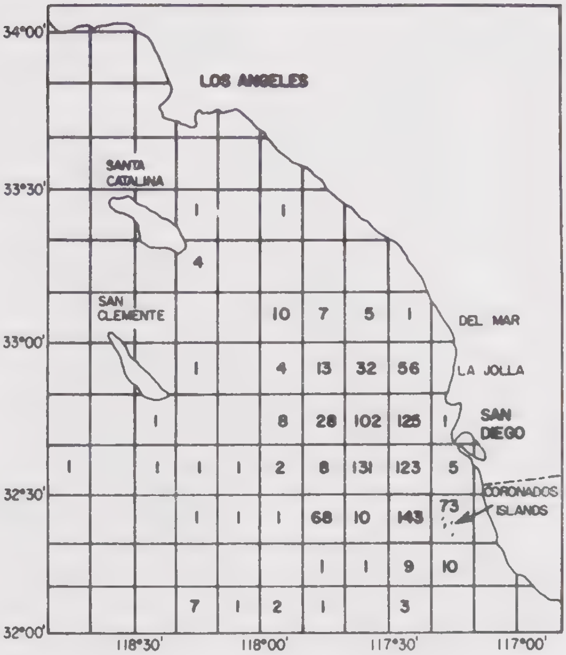
2 5 69 33 13 13
5 7 32 27 75 140 77
1 7 15 50 79 248 371 190
1 1 3 7 60 96 409 378 40
1 4 9 78 95 630 173
2 9 66 22 1
9 2 2 1 3

Figure 2.—Catch distribution of striped marlin landed at San Diego, California; August, September, and October 1963 through 1967.

and lat. 33°00′ N, long. 117°50′ W, and the coast from near Del Mar, California, to Rosarita Beach, Baja California, Mexico. This area accounted for 76.4% of all fish landed in these months at the San Diego Marlin Club.

CATCH AND TEMPERATURE RELATIONSHIP

Since August 1963, the National Marine Fisheries Service, Tiburon Coastal Fisheries Research Laboratory, Tiburon, California, has conducted once each month sea surface temperature survey flights off southern California in cooperation with the U.S. Coast Guard. These surveys are conducted from an aircraft using an infrared radiation thermometer (ART) to measure sea surface temperatures (Squire, 1972), and data are published in the form of isotherm charts. Comparison of 146 simultaneous sea surface temperature observations between the airborne instrument and a sea surface bucket cast showed an average difference of 0.35° F (0.2° C) (ART lower), a range of −1.9° F (1.1° C) to 1.2° F (0.7°C), and a standard deviation of 0.65° F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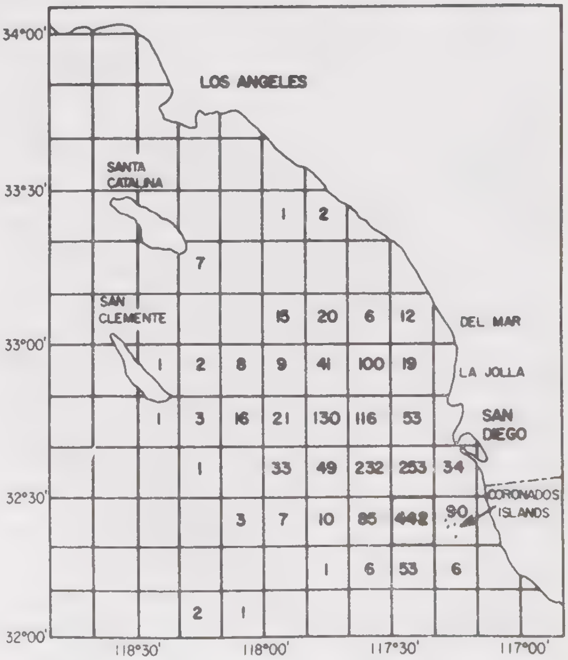
1 1
4
10 7 5 1
1 4 13 32 56
1 8 28 102 125 1
1 1 1 1 2 8 131 123 5
1 1 1 68 10 143 73
1 1 9 10
7 1 2 1 3

Figure 3.—Catch distribution for August 1963 through 1967.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7
15 20 6 12
1 2 8 9 41 100 19
1 3 16 21 130 116 53
1 33 49 232 253 34
3 7 10 85 442 90
1 6 53 6
2 1

Figure 4.—Catch distribution for September 1963 through 1967.

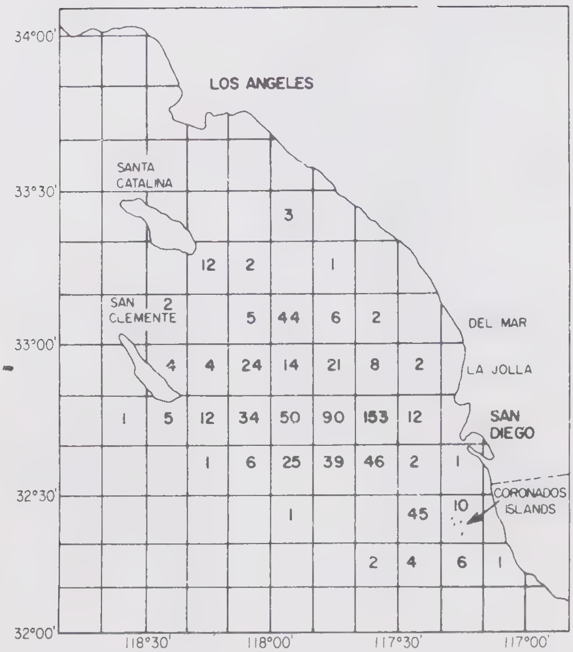

Figure 5.—Catch distribution for October 1963 through 1967.

Table 2.—Mean catch temperatures and numbers of striped marlin landed at the San Diego Marlin Club; August, September, October 1963 through 1967. Mean temperatures calculated from subjective temperature data and catch data for each 10-minute longitude by latitude block area.

Month	Year	Mean temp/month	# fish
August	1963	67.7° F (19.8°C)	605
	1964	68.0° F (20.0°C)	78
	1965	64.1° F (17.8°C)	25
	1966	71.2° F (21.8°C)	102
	1967	66.3° F (19.0°C)	194
September	1963	67.8° F (19.0°C)	717
	1964	69.3° F (20.7°C)	361
	1965	65.0° F (18.3°C)	124
	1966	67.0° F (19.4°C)	335
	1967	69.1° F (20.8°C)	354
October	1963	72.2° F (22.5°C)	73
	1964	66.5° F (19.1°C)	339
	1965	65.2° F (18.4°C)	147
	1966	69.0° F (20.8°C)	98
	1967	67.9° F (19.9°C)	43

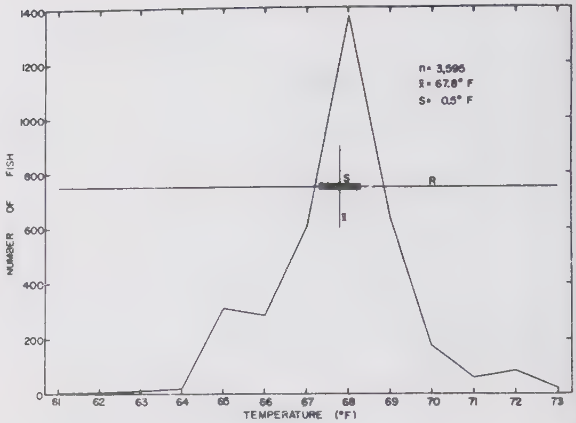

Figure 6.—Distribution of striped marlin catch by sea surface temperature showing the mean ($\bar{x}$), standard deviation (S), and range (R) of temperatures for all catches landed at the San Diego Marlin Club, California (1963-1967).

(0.36° C). From these isotherm charts a sea surface temperature value was estimated for each 10-minute block area where fish were caught as shown in Figures 3-5. Using these temperature data and the catch distribution data for the 10-minute block area, mean catch-temperature[2] figures were computed for striped marlin landed in August, September, and October for the period 1963-1967 (Table 2). Mean catch-temperatures by month for all fish landed were: August, 67.8° F (19.9° C); September, 68.0° F (20.0°C); and October, 67.3° F (19.6°C). Temperatures at which striped marlin were caught ranged from 61.0° F (16.1° C) to 73.0° F (22.8° C) with a mean overall catch temperature of 67.8° F (19.9° C) and a standard deviation of 0.5° F (0.9° C). The distribution of the catch relative to temperature for all catches is shown in Figure 6.

OBSERVATIONS OF TEMPERATURE ISOTHERMS OFF SAN DIEGO AND BAJA CALIFORNIA RELATIVE TO FISHING SUCCESS

For comparison of marlin catch to sea surface temperature for the period 1963 to 1970, temperature data for the area from southern California to off he central west coast of Baja California were ob-ained from half-month average sea surface sotherm charts published by the National Marine Fisheries Service (U. S. Bureau of Commercial Fisheries, 1961). These isotherm charts are computed from sea surface temperatures reported by ships in the eastern Pacific. From examination of these isotherm charts temperatures off San Diego and to the south toward central Baja California were highest during the fishing seasons of 1963 and 1967, and lowest during the 1965 season (catches of 1,410, 602, and 296 respectively).

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[2] Each striped marlin had a temperature value associated with it; the mean catch-temperature was computed by summing the temperature values and dividing by the total number of entries.

Of particular interest to fishermen is the time of the beginning of the fishing season. Early in the fishing season off San Diego during the period prior to an increase in sea surface temperature to 68° F (20.0°C) the total number of marlin caught was 115, 2.5% of the total catch of 4,535 fishes (1963-1970), whereas for the first half-month period of each year showing the 68° F (20.0° C) isotherm off San Diego. the catch totaled 824 fish, representing an increase to 18.2% of the total catch.

During the half-month periods, data show that temperatures were below 68°F (20.0° C) for 23 periods, and during this time a total of 931 fish, or an average of 40.5 fish/period, were caught. Temperatures were between 68° F (20.0° C) and 69.9° F (21.0° C) during 15 periods, and 1,886 fish were caught, resulting in an average catch of 99.2 fish/period. Temperatures of 70° F (21.0° C) or above for 14 periods resulted in a catch of 1,718 fish or an average catch of 122.7/period.

The numbers of marlin caught during the half-month periods when the 68° F (20.0° C) and 70° F (21.0° C) isotherms were continuous from off Baja California northward to off southern California were compared to the catch when these isotherms were discontinuous (Table 3). For examples of continuous and discontinuous isotherms in the area of study, see Figure 7.

Data show that during periods when the 68° F (20.0° C) or 70° F (21.1° C) average isotherms were continuous from off central Baja California northward to off southern California, a total of 2,046 fish was caught for an average catch/period of 146.1 fish, whereas a total of 1,599 fish was caught for an average catch of 82.0/period when these isotherms were discontinuous. During periods when the 70° F (21.1° C) average isotherm was continuous the largest catch per any period (570 fish) and the highest average catch rate/period (205.3 fish) was recorded.

Table 3.—Comparison of catch and catch rates during periods of continuous and discontinuous 68° (20.0°C) and 70° F (21.1°C) isotherms.

	68°F (20.0°C)	70°F (21.1°C)	Totals
Discontinuous Isotherms			
Catch	1,072	486	1,559
No. of periods	11	8	19
Av. catch/period	97.4	61.7	82.0
Continuous Isotherms			
Catch	814	1,232	2,046
No. of periods	8	6	14
Av. catch/period	101.7	205.3	146.1

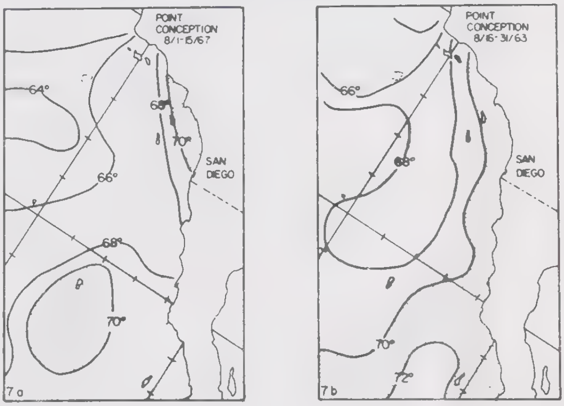

Figure 7.—Examples of discontinuous isotherms (7a) and continuous isotherms (7b) in the area of study.

From examination of the temperature structure of the waters off northern Baja California and southern California based on half-month average temperature charts it appears that 1) initial warming of the waters to an average temperature of 68° F (20.0° C) is related to an increase in catch, 2) continuity of the 68° F (20.0° C) or 70° F (21.1° C) average isotherms from off central Baja California northward to off southern California was associated with higher catches compared to catches when these isotherms were discontinuous.

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Migration Patterns of Istiophoridae in the Pacific Ocean as Determined by Cooperative Tagging Programs

JAMES L. SQUIRE, JR.[1]

ABSTRACT

Since 1954, billfish have been tagged by cooperative marine game fish tagging programs in many of the major sportfishing areas of the Pacific. Major locations of tagging have been off southern California, U.S.A., Baja California Sur and mainland Mexico, Panama, and Australia. Two cooperative marine game fish tagging programs have operated in the Pacific, 1) the Cooperative Marine Game Fish Tagging Program, sponsored jointly by the Woods Hole Oceanographic Institution and the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, and 2) a cooperative program conducted by the California Department of Fish and Game.

During 1954-1971, 15,540 billfish were tagged. Records show 9,849 striped marlin *(Tetrapturus audax)*, 4,821 sailfish *(Istiophorus platypterus)*, 622 black marlin *(Makaira indica)*, and 248 blue marlin *(Makaira nigricans)* were tagged during this period. Ninety-seven tag recoveries have been made; these include 85 striped marlin, 10 sailfish, and 2 black marlin. Eighty-one percent of these recoveries were by longline fishing vessels, the remainder by marine sport fishermen.

The tag recovery rates were 0.88% for striped marlin, 0.32% for black marlin, and 0.24% for sailfish.

Four types of tags were used in the two programs. Two types of metal tip dart tags were used by the Woods Hole Oceanographic Institution; metal tipped single- and double-barbed plastic dart tags were used by the National Marine Fisheries Service; and a single-barb plastic dart tag was used by the California Department of Fish and Game. Tag types giving the best recovery rate for striped marlin and sailfish were the plastic single- and double-barbed dart tags.

Recovery data for striped marlin tagged in the eastern Pacific show a movement away from the tip of Baja California in a south to southwest direction in late spring and early summer. Some recoveries were made of fish tagged near the tip of Baja California and recaptured northwest of the tip of Baja California, Mexico. The migration pattern to the south and southwest at this time of the year may be related to spawning. Striped marlin tagged off southern California show a migration to the south in late summer and early fall. Recoveries of striped marlin in the eastern Pacific were generally short-term (average of 89 days) and covered short distances, averaging 281 nautical miles. Only three of 85 tagged striped marlin, and one of two tagged black marlin, were recovered 1,000 nautical miles or more from the site of tagging. The few recoveries of tagged black marlin (2) and sailfish (10) did not provide sufficient data to determine migration patterns for these species.

The tagging or marking of fish is an established method in the study of fish growth, migration, distribution and population structure (Schaefer, Chatwin, and Broadhead, 1961; Beckett, 1970). The concept of utilizing the services of marine anglers in the tagging of large marine game fishes, such as tunas and billfishes, was developed by Frank J. Mather III of the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. The first cooperative tagging of billfishes in the Pacific Ocean was in 1954 when tagging equipment was furnished by Mather to anglers fishing for billfishes and tunas. Interest in the tagging and releasing of billfishes in the Pacific increased and in 1961 arrangements were made with Mather for the then U.S. Fish and Wildlife Service's Tiburon Marine Laboratory to assume responsibility for the cooperative Marine Game Fish Tagging Program in the Pacific area. This program has recently been transferred to the Department of Commerce, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory, La Jolla, California. The Pacific phase of the Cooperative

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[1] NOAA, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

Game Fish Tagging Program was assisted by the International Game Fish Association and the Department of Fisheries, Mexico.

The State of California, Department of Fish and Game also participated in a cooperative tagging program for billfishes (striped marlin and sailfish) from 1965 through 1970 with the assistance of anglers representing the Oceanic Research Institute, San Diego, California.

The importance of the istiophorid billfishes, such as striped marlin *(Tetrapturus audax)* and sailfish *(Istiophorus platypterus)* in the eastern Pacific, blue marlin *(Makaira nigricans)* about the Hawaiian Islands (Strasburg, 1969), and black marlin *(Makaira indica)* off Queensland, Australia and throughout the Pacific, as species on which valuable sport fisheries are based upon, is well known. In addition to an extensive sportfishery, these species also assist in supporting an extensive commercial longline fishery throughout the subtropical and tropical Pacific.

The cooperative billfish tagging programs in the Pacific were developed to obtain an adequate understanding of the migratory patterns of billfishes so that ultimately the stocks can be properly managed. The migratory patterns of billfishes in the Pacific are little known. These fishes are caught in quantity primarily with hook and line, either by longlining or by rod and reel. Use of the more efficient longline gear from a research vessel for the purpose of tagging and releasing of billfishes would be costly, and in excess of any funds now available for billfish migration studies. The aid of the marine game fish angler was requested and to date the cooperative tagging programs have accounted for nearly all the billfishes tagged in the Pacific. Bayliff[2] reported tagging of billfishes by research agencies such as the National Marine Fisheries Service, Honolulu Laboratory and the Kanagawa Prefectural Fisheries Research Station in Japan. In 1968 the Honolulu Laboratory tagged 44 striped marlin, 1 blue marlin, and 10 shortbill spearfish. The Japanese Research Station reported tagging 33 striped marlin, 3 blue marlin, and 73 broadbill swordfish *(Xiphias gladius)*. No returns were reported from any of these taggings.

By furnishing tagging equipment to marine game fish anglers who have an interest in the rational conservation of the billfish resources, substantial numbers of billfishes can be tagged in areas of intensive sportfishing for a relatively modest cost. Marine game fishermen have been encouraged to tag and release billfishes through information in the form of written requests, talks before billfishing clubs, posters, and brochures. In addition, posters requesting both sport and commercial fisheries to return tags and advising of a reward are distributed in both the Spanish and Japanese languages.

The major geographical locations of cooperative tagging have been about the tip of Baja California, Mexico; Mazatlán, Mexico; and Cairns, Australia. Other locations where lesser numbers of tagged fish have been released are off southern California and the Hawaiian Islands, U.S.A.; Manzanillo and Acapulco, Mexico; Piñas Bay, Panama; Salinas, Ecuador; Tahiti; and New Zealand.

MATERIALS AND METHODS

The large size and active nature of billfishes require a tag that can be applied while the fish remains in the water. Dart tags were selected because they could be used effectively by billfish anglers inexperienced in tagging fish. All tagging, with the exception of a few striped marlin and swordfish, have been on hook and line caught fish. Some surface-swimming billfishes have been free-tagged by harpooning with a dart tag.

Four types of tags were used by the cooperative programs. The California Department of Fish and Game used the single nylon barb tag with yellow polyvinylchloride tubing bearing the legend, type FT-1 (Fig. 1A). The National Marine Fisheries Service's cooperative program used four types of dart tags: (i) In 1963 a number of type "C" tags (Fig. 1C) were issued. These tags had a stainless steel tip with yellow polyvinyl tubing for the legend and were similar to the type of tags used by the Woods Hole Oceanographic Institution program in the late 1950's and early 1960's. (ii) The FT-1 (Fig. 1A) with a slightly enlarged base on the dart head to prevent the tagging applicator tube from shearing the barb when pressure is applied to insert the tag into the billfish. This tag was recommended for tagging sailfish. (iii) A larger double barbed nylon tag FM-67 (Fig. 1B) with yellow polyvinyl tubing for information was used from 1963 to 1971. (iv) In mid-1971, the stainless steel dart tag, type "H" (Fig. 1D) was introduced. This tag has a nylon, monofilament line extending from the stainless steel barb with a yellow polyvinyl tubing sleeve over the

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[2] Bayliff, William H., et al. 1972. Second interim report of the Working Party on Tuna and Billfish Tagging in the Pacific and Indian Oceans. FAO, unpublished.

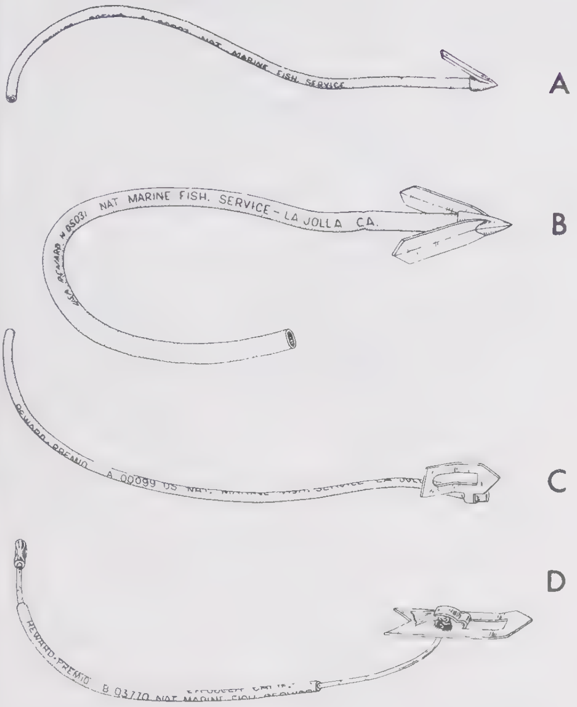

Figure 1.—Types of dart tags used by the cooperative tagging programs.

monofilament for printed information. All tags used by the National Marine Fisheries Service and the California Department of Fish and Game were manufactured by the Floy Tag Manufacturing Company, Seattle, Washington.[3] On all the tags, a serial number and a message are heat-embossed in black. The legend gives an address for return, together with a notice that a reward will be given. In the early years of the cooperative program the Woods Hole Oceanographic program used the type "C" tags (Fig. 1C) in the Pacific. In later years tags of an "H" type were used (Fig. 1D).

Upon bringing the billfish close to the boat the angler was instructed to insert the tag beside the dorsal fin, just posterior of the first dorsal ray, and at an angle so the tubing points in the general direction of the tail. This was done to provide a streamlining effect of the water flow over the tubing. After insertion, the leader was to be cut, thereby releasing the fish and leaving the hook and a portion of the leader attached. If necessary, it was recommended that the billfish be towed forward slowly before release to provide an additional supply of oxygen to assist in reviving the fish.

Tags were attached to a postcard having the serial number of the tag. After tagging the angler was requested to complete the information on tagging date, location, species, estimate of weight, tagger's name and address, and return it to the organization issuing the tag.

TAGGING RESULTS

In the early 1960's, the Japanese longline fleet began fishing near the coasts of North, Central, and South America. The advent of this fishery has provided an invaluable source of billfish tag recoveries. Prior to 1963, a good source of recovery for billfish tags had not existed in the eastern Pacific.

Cooperating marine game fish anglers have tagged 15,540 billfishes in the Pacific since 1954.

Woods Hole Oceanographic Institution records for the period 1954 through 1971, show 3,618 tagged billfish releases (Mather, 1972). The National Marine Fisheries Service program resulted in the tagging and release of 10,964 billfishes. The distribution of tagging effort for the 14,582 billfish tagged by the Woods Hole Oceanographic Institution/National Marine Fisheries Service Cooperative Marine Game Fish Tagging Program included 8,953 striped marlin, 248 blue marlin, 622 black marlin, and 4,759 sailfish. The State of California Department of Fish and Game conducted a cooperative tagging program with selected billfish anglers and this program functioned during the period 1965-1970. Of a total of 958 billfishes tagged, 896 were striped marlin and 62 sailfish.

A total of 9,849 striped marlin, 622 black marlin, 248 blue marlin, and 4,821 sailfish was tagged by the cooperative programs. The totals and numbers of the four species of billfishes tagged per year and the number of recoveries (for each year's tagging) are listed by tagging organization in Table 1.

Recoveries

Between 1954 and 1963, no returns were reported in the Pacific for the 945 billfishes tagged and released. From 1963 through 1971 a total of 97 tagged billfishes was recaptured. Foreign longliners recorded 79 recoveries or 81% of the total. One of these was by a Taiwanese longliner; the others were recovered by Japanese longliners. Marine game fishermen have accounted for 18 recoveries or 19%

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[3] Use of a trade name does not imply endorsement by the National Marine Fisheries Service.

Table 1.—Billfishes tagged and recaptured in the Pacific by cooperative marine game fish tagging programs.

		Species				
Year	Organization	Striped marlin	Black marlin	Blue marlin	Sailfish	Totals
1954	A_1	—	—	—	0/3	0/3
1955	A_1	—	—	—	0/9	0/9
1956	A_1	—	—	—	—	—
1957	A_1	0/17	—	—	0/35	0/52
1958	A_1	0/13	—	—	0/8	0/21
1959	A_1	0/10	—	—	0/124	0/134
1960	A_1	0/2	—	—	0/104	0/106
1961	A	0/87	0/8	—	0/188	0/283
1962	A_1	0/76	0/4	—	0/257	0/337
1963	A_1	1/942	0/37	0/30	0/266	0/1,275
	A_2	0/532	0/1	0/18	0/26	0/577
	B	0/18	—	—	—	0/18
1964	A_1	1/113	0/36	0/12	0/241	1/402
	A_2	4/281	—	0/3	0/268	4/552
	B	4/329	—	—	0/7	4/336
1965	A_1	1/52	0/26	0/4	0/233	1/315
	A_2	6/431	0/6	0/7	2/167	8/611
	B	0/253	—	—	0/18	0/271
1966	A_1	0/47	0/19	0/1	0/124	0/191
	A_2	10/735	—	—	2/283	12/1,018
	B	2/186	—	—	0/31	2/217
1967	A_1	0/31	0/27	—	0/62	0/120
	A_2	19/1,279	0/3	0/23	1/480	20/1,785
	B	0/107	—	—	0/1	0/108
1968	A_1	1/29	0/31	—	0/98	1/158
	A_2	13/1,119	0/13	0/32	2/432	15/1,596
	B	—	—	—	—	—
1969	A_1	0/5	0/36	—	0/78	0/119
	A_2	4/747	1/39	0/31	0/318	5/1,135
	B	1/1	—	—	—	1/1
1970	A_1	0/6	0/19	0/2	0/33	0/60
	A_2	16/989	0/82	—	2/501	18/1,572
	B	0/2	—	—	1/5	1/7
1971	A_1	0/9	—	0/12	0/12	0/33
	A_2	2/1,401	1/235	0/73	0/409	3/2,118
Also 1 shortbill spearfish *(Tetrapturus angustirostris)* tagged						
	B	—	—	—	—	—
Totals		85/9,849	2/622	0/248	10/4,821	97/15,540

NOTE: Releases (right of slash). returns (left of slash) by organization conducting the tagging. Returns are listed by year of recapture for WHOI, NMFS and CF&G lists recapture by year of tagging.

A. Cooperative Marine Game Fish Tagging Program.
A_1 Woods Hole Oceanographic Institution, from 1954.
A_2 National Marine Fisheries Service, from 1963.
B. California Department of Fish and Game.

of the total. The FM-67 and FT-1 tags are buoyant and a number of these have been returned after being picked up on the beach after being used to tag a billfish. These tags may have been lost overboard during the tagging process or may have been shed after tagging. Recoveries were considered valid only when the tag was taken from a recently caught fish.

The Cooperative Marine Game Fish Tagging program (National Marine Fisheries Service —Pacific) issued a conservation certificate to both the tagger and recoverer. A cash reward was paid to the tag recoverer by all three programs.

Table 2 gives the percentage rate of recovery by program, by year, and total recovery rate for each species and for all billfish tagged. Table 3 gives a summation of the rate of return for each of the three cooperative tagging programs.

Tag Performance

For the four types of tags used by the cooperative programs (FT-1, FM-67, C, and H) a comparison of tag performance can be made for the types FT-1 used by the California Department of Fish and Game, and the National Marine Fisheries Service and the Woods Hole Oceanographic Institution.

Recovery data for 10,777 tags used by the National Marine Fisheries Service Cooperative Tagging program and 958 tags used by the California

Department of Fish and Game to tag striped marlin, black marlin, and sailfish were analyzed for the purpose of giving some indication of tag performance. Eighty-two percent of the billfishes were tagged with FM-67 tags, 13.8% with FT-1 tags, 3.4% with the "H" tags, and 0.8% with the "C" tag. There were no recoveries of the "C" tag, and the "H" tag has been used only since mid-1971. The percentage recovery rate by tag type and tagging organization is listed in Table 4.

Table 2.—Rate of recovery of tagged billfishes.

		Species				
Year	Organization	Striped marlin	Black marlin	Blue marlin	Sailfish	Overall % recovery rate
1963	A_1	0.11%	0.00%	0.00%	0.00%	0.08%
	A_2	0.00	0.00	0.00	0.00	0.00
	B	0.00	—	—	—	0.00
				Annual Overall		0.05%
1964	A_1	0.88	0.00	0.00	0.00	0.25
	A_2	1.42	—	0.00	0.00	0.72
	B	1.21	—	—	0.00	1.20
				Annual Overall		0.70%
1965	A_1	1.92	0.00	0.00	0.00	0.32
	A_2	1.40	0.00	0.00	1.20	1.31
	B	0.00	—	—	0.00	0.00
				Annual Overall		0.75%
1966	A_1	0.00	0.00	0.00	0.00	0.00
	A_2	1.40	—	—	0.71	1.08
	B	1.07	—	—	0.00	0.92
				Annual Overall		0.91%
1967	A_1	0.00	0.00	—	0.00	0.00
	A_2	1.50	0.00	0.00	0.21	1.12
	B	0.00	—	—	0.00	0.00
				Annual Overall		0.99%
1968	A_1	3.44	0.00	—	0.00	0.63
	A_2	1.16	0.00	0.00	0.46	0.94
	B	—	—	—	—	—
				Annual Overall		0.91%
1969	A_1	0.00	0.00	—	0.00	0.00
	A_2	0.53	2.56	0.00	0.00	0.35
	B	100.00	—	—	—	100.00
				Annual Overall		0.40%
1970	A_1	0.00	0.00	0.00	0.00	0.00
	A_2	1.62	0.00	—	0.40	1.15
	B	0.00	—	—	20.00	14.28
				Annual Overall		1.16%
1971	A_1	0.00	—	0.00	0.00	0.00
	A_2	0.14	0.43	0.00	0.00	0.14
	B	—	—	—	—	—
				Annual Overall		0.13%
Totals						
1954-71		0.86%	0.32%	0.00%	0.21%	0.62%
1963-71		0.88%	0.32%	0.00%	0.24%	0.66%

A_1 = Cooperative Marine Game Fish Tagging, Woods Hole Oceanographic Institution.
A_2 = Cooperative Marine Game Fish Tagging, National Marine Fisheries Service.
B = Cooperative Billfish Tagging, California Department of Fish and Game.
— = no billfish tagged.
1954 through 1962 no recoveries reported.

Hooking mortality undoubtedly accounts for a high tag loss, in addition to unknown losses that occur through tag shedding. The percentage of tag loss for the several types of tags is not known.

MIGRATORY PATTERNS

Eastern Pacific

Figures 2, 3, 4, and 5 show the tagging and recovery points by quarters for both striped marlin and sailfish in the eastern Pacific. The recovery data from the longline fleet have not been adjusted for fishing effort in the various geographical areas. The commercial longline fishery has expanded to the limits of the fishery in the eastern Pacific and the seasonal distribution of fishing effort is assumed to

Table 3.—Rate of recovery (left figure refers to number of tag recoveries; right figure refers to number of fish tagged and released).

Year	Striped marlin	Black marlin	Blue marlin	Sailfish	Total
Program A_1—Woods Hole Oceanographic Institution					
1954-1971	4/1,439 = 0.28%	0/243 = —%	0/61 = —%	0/1,875 = —%	4/3,618 = 0.11%
Since 1963	4/1,234 = 0.32%	0/231 = —%	0/61 = —%	0/1,147 = —%	4/2,673 = 0.15%
Program A_2—National Marine Fisheries Service					
1963-1971	74/7,514 = 0.98%	2/379 = 0.53%	0/187 = —%	9/2,884 = 0.31%	85/10,964 = 0.78%
Program B—California Department of Fish and Game					
1963-1970	7/896 = 0.78%	—/— = —%	—/— = —%	1/62 = 1.6%	8/958 = 0.84%

Rates of recovery for striped marlin and sailfish combined, 1963-1971:
Program A_1 4/2,673 = 0.15%
A_2 85/10,964 = 0.78%
B 8/958 = 0.84%

Table 4.—Percentage recovery rates for tag types used by the California Department of Fish and Game (CF&G), and National Marine Fisheries Service (NMFS), fish tagged through 1971.

Species	Agency	Type tag	% recovery	
Striped marlin	NMFS	FM67	1.06%	>0.66%
	NMFS	FT-1	0.42	
	CF&G	FT-1	0.80	
	NMFS	H	0.40	
Black marlin	NMFS	FM67	0.32%	
	NMFS	H	1.20	
Sailfish	NMFS	FM67	0.30%	>0.86%
	NMFS	FT-1	0.60	
	CF&G	FT-1	1.60	

be located in areas of greatest concentration and maximum yield.

January, February, March.—During this period striped marlin are commonly taken by the sportfishery off Mazatlán, Mexico, and in lesser numbers off Cabo San Lucas, the southern tip of Baja California Sur, Mexico. Sailfish are not common in the area about the mouth of the Gulf of California during the winter and early spring. The longest distance recovery of a striped marlin was for a fish tagged near the tip of Baja California Sur, Mexico, and recovered 200 nautical miles southwest of the Hawaiian Islands, a distance of 3,120 nautical miles in a period of 3 mo (2/67-5/67). Recoveries of striped marlin tagged off Mazatlán, Mexico, show a west to southwest movement towards the tip of Baja California Sur, and the Revillagigedo Islands, Mexico, respectively. Recoveries of striped marlin tagged about the tip of Baja California Sur, Mexico, show some movement toward the northwest and northeast; however the direction of the movement as indicated by tag recoveries from this area is south through southeast (reference, Fig. 2).

April, May, June.—During late spring and early summer the sportfishery striped marlin catch decreases off Mazatlán and increases about the tip of Baja California Sur, Mexico. Sailfish becomes the dominant species off Mazatlán during this season. A pattern of striped marlin movement, indicated by recoveries, is from about the tip of Baja California southward toward Las Tres Marias and Revillagigedo Islands, Mexico. Striped marlin tagged

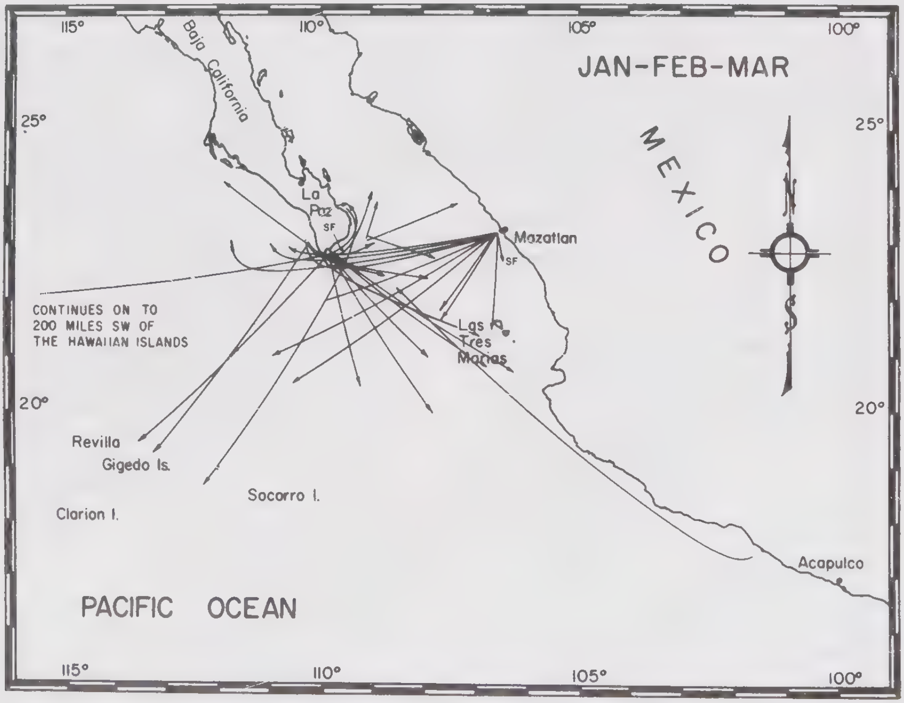
115°
110°
105°
100°
JAN-FEB-MAR
Baja California
25°
25°
MEXICO
La Paz
SF
Mazatlan
SF
N
S
CONTINUES ON TO
200 MILES SW OF
THE HAWAIIAN ISLANDS
Las Tres Marias
20°
20°
Revilla Gigedo Is.
Socorro I.
Clarion I.
Acapulco
PACIFIC OCEAN
115°
110°
105°
100°

Figure 2.—Movements of billfishes from tagging conducted during the months of January, February, and March. Striped marlin unless otherwise noted as SF (sailfish).

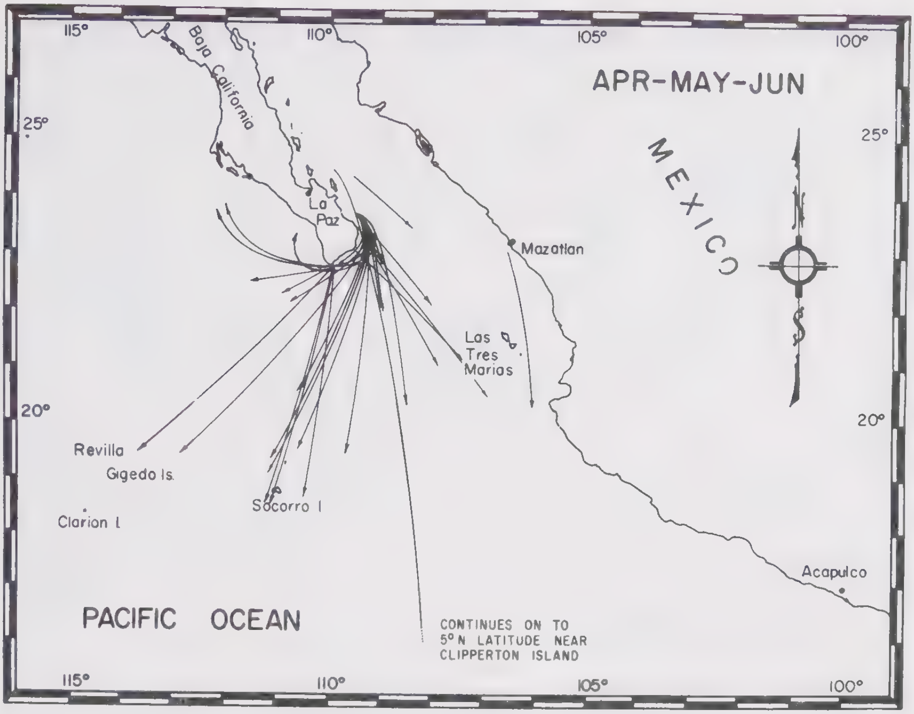
115°
110°
105°
100°
APR-MAY-JUN
Baja California
25°
MEXICO
La Paz
Mazatlan
Las Tres Marias
20°
Revilla Gigedo Is.
Socorro I
Clarion I.
Acapulco
PACIFIC OCEAN
CONTINUES ON TO 5° N LATITUDE NEAR CLIPPERTON ISLAND

Figure 3.—Movements of striped marlin from tagging conducted during the months of April, May, and June.

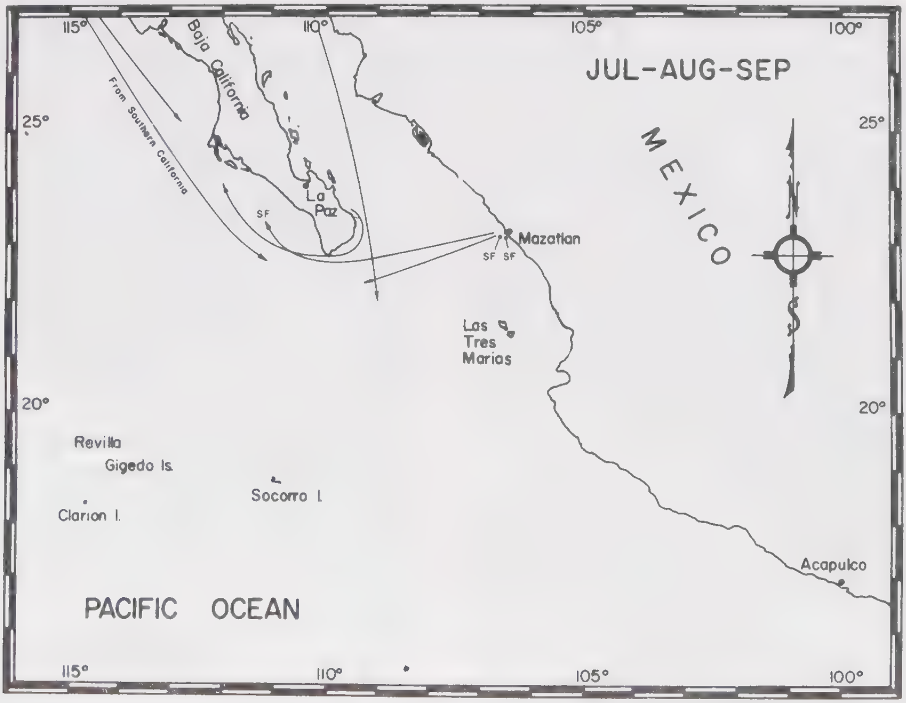
115°
110°
105°
100°
JUL-AUG-SEP
Baja California
From Southern California
25°
MEXICO
La Paz
SF
Mazatlan
SF SF
Las Tres Marias
20°
Revilla Gigedo Is.
Socorro I.
Clarion I.
Acapulco
PACIFIC OCEAN

Figure 4.—Movements of billfishes from tagging conducted during the months of July, August, and September. Striped marlin unless otherwise noted as SF (sailfish).

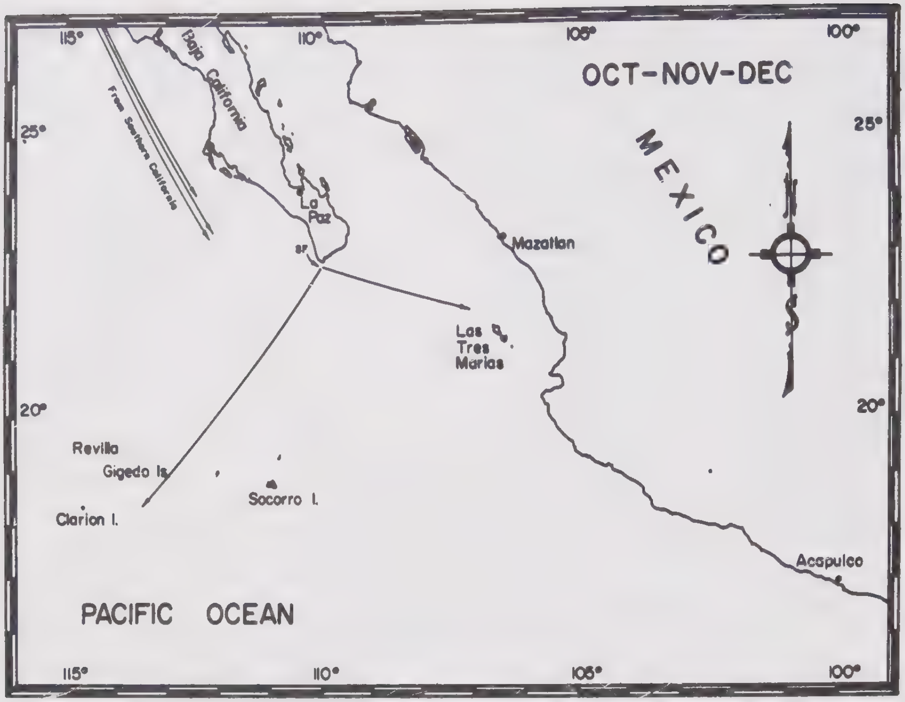

Figure 5.—Movements of billfishes from tagging conducted during the months of October, November, and December. Striped marlin unless otherwise noted as SF (sailfish).

along the east side of the tip of Baja California have shown some movement about the tip to the west and northwest. The longest southward migration of any tagged striped marlin was recorded during this period; the marlin's total straight line migration was 1,153 nautical miles from near the tip of Baja California to near Clipperton Island in 71 days (reference, Fig. 3).

July, August, September.—A reduction in tagging effort due to fewer sportfishermen traveling to the tip of Baja California and the west coast of Mexico during the warm season is reflected in the numbers of billfishes tagged and later recovered. Short distance sailfish recoveries were made near Mazatlán. A sailfish, tagged during this period off Mazatlán, was recovered northwest of the tip of Baja California, a distance of 250 nautical miles, after 457 days. This sailfish recovery was the greatest in distance and time (reference, Fig. 4).

Striped marlin fishing becomes productive off southern California in late August and two recoveries were made off the southern west coast of Baja California of striped marlin tagged off southern California in September. One recovery was made of a striped marlin tagged off Guaymas, Mexico, which is located on the east coast in the upper Gulf of California, and recaptured south of the tip of Baja California 17 days later.

October, November, December.—This is a period of reduced tagging throughout all eastern Pacific sportfishing areas. A limited amount of tagging off southern California has yielded returns, one being the second longest return recorded, 2,090 nautical miles to the southwest in 179 days. Three recoveries of striped marlin tagged off southern California were recovered northwest of the tip of Baja California 1 to 4 months later (reference, Fig. 5).

As in any conventional tagging or marking program only two points in the migration are known —the location of tagging and the tag recovery point. The geographical migratory course of the billfish between these two points is unknown.

Southwestern Pacific

Through the cooperation of anglers fishing for black marlin near Cairns, Queensland, Australia, recoveries of two tagged black marlin have been recorded (Fig. 6). One was recovered by a Japanese

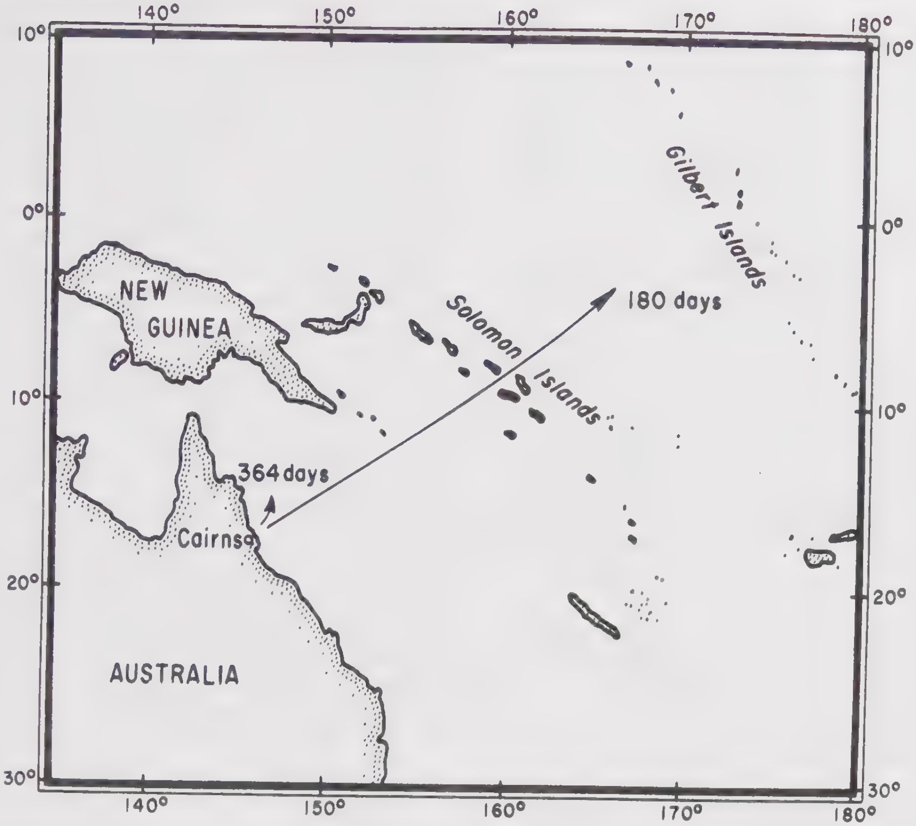
140°
150°
160°
170°
180°
10°
0°
10°
20°
30°
NEW GUINEA
Solomon Islands
Gilbert Islands
180 days
364 days
Cairns
AUSTRALIA

Figure 6.—Movements of black marlin tagged off Queensland, Australia.

longliner 364 days after tagging about 90 nautical miles north from the point of tagging near Hope Reef, Queensland, Australia. The second was recovered 180 days after tagging by a Taiwanese longliner 1,440 nautical miles northeast of the tagging site at Escape Reef, Queensland, Australia.

MIGRATION RATES AND TIMES

The speed of migration of striped marlin, expressed in nautical miles per day projected on a straight line/time basis, varies considerably between local and distant water recoveries (Fig. 7). For billfishes tagged off the Baja California/ Mazatlán area the average time at liberty was 94 days. An average distance of 176 nautical miles traveled equals 1.9 nautical miles per day. Striped marlin tagged off southern California recovered near the tip of Baja California had an average release time of 52 days and a migration rate of 12.3 nautical miles per day. Other long distance migration rates are as follows; southern California to southwest of the Hawaiian Islands, 26.0 nautical

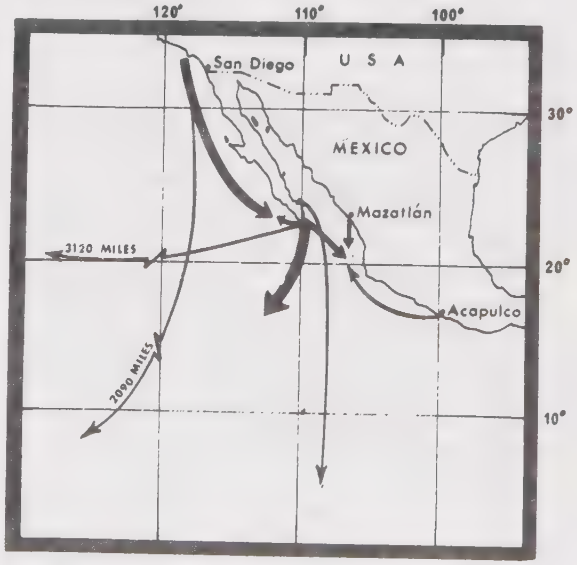
120°
110°
100°
San Diego
U S A
MEXICO
Mazatlán
Acapulco
3120 MILES
2090 MILES
30°
20°
10°

Figure 7.—General migration patterns of striped marlin tagged off southern California and Mexico.

miles per day; tip of Baja California to ⅔ the distance to the Hawaiian Islands, 11.7 nautical miles per day; tip of Baja California to near Clipperton Island, 16.3 nautical miles per day.

For all striped marlin recoveries having accurate records, the average days out is 89; the average migration 281 nautical miles, and average distance per day out, 3.16 nautical miles.

For the limited number of sailfish recaptured the average number of days out was 113, the migration rate was 0.4 nautical miles per day. The longest distance recorded for any sailfish was 250 nautical miles in 457 days out. This was the longest release-recapture time of any billfish tagged in the Pacific.

Two black marlin were recovered, one near the point of tagging in the Coral Sea 364 days after tagging, the other 180 days after tagging, 1,440 nautical miles northeast of Queensland, Australia. This billfish averaged 8 nautical miles per day.

The greatest migration rate in nautical miles per day for any billfish was a short-term recovery of a striped marlin tagged off the tip of Baja California which averaged 31.6 nautical miles per day.

DISCUSSION AND SUMMARY

The concept of utilizing cooperating marine game fish anglers to tag and release billfishes has proven to be a practical approach to the study of billfish migration patterns.

Experience indicates that accurate estimates of weights and lengths of tagged fish cannot be expected.

After tagging, the angler is requested to return the tag card. In 1968 a comparison was made of the number of tags returned with a matching tag card on file, with those that did not have a tag card. This indicated that about 17% of the tag cards were not being returned. As a result, an active campaign to have the angler return the cards was begun.

The number of billfishes tagged annually in the Pacific has steadily increased since 1954, reaching a total of 2,118 in 1971. The annual rate of billfish recoveries rose to above the 0.90% level from 1966 through 1968, dropped to 0.40% in 1969, increased to a peak of 1.16% in 1970, and dropped to a very low 0.13% in 1971. The reason for the sharp decline in recoveries in 1971 cannot be explained. The only change in operation of the National Marine Fisheries Service program was the introduction of the "H" type tag. During the latter half of 1971, 317 "H" tags were used, which equalled only 14.7% of the total tags used by the National Marine Fisheries Service program during 1971.

The recovery rate from FM-67 and FT-1 tags used by the National Marine Fisheries Service and California Department of Fish and Game in the Pacific for striped marlin were comparable. The California Department of Fish and Game program obtained a 0.80% recovery rate using the FT-1 and the National Marine Fisheries Service program obtained a 0.42% recovery rate using the same tag, giving an overall average of 0.66%. The California Department of Fish and Game program restricted its tag distribution to a limited number of experienced anglers fishing from private boats. On an average these anglers were more experienced in tagging billfish than most of the anglers participating in the National Marine Fisheries Service program. The FM-67 tag used for striped marlin shows a greater recovery rate (1.06%) than any of the four types of tags used. The recovery rate of the California Department of Fish and Game FT-1 tag (0.80%) was near that of the FM-67.

The National Marine Fisheries Service program changed to the metal-plastic "H" type tag in mid-1971 because of the recovery record (recovery percent and time out) for white marlin *(Tetrapturus albidus)* and sailfish in the Atlantic Ocean experienced by the Woods Hole Oceanographic Institution program.

Although many factors such as seasons and areas of fishing and economic value of billfishes influence catch rates in the Atlantic and eastern Pacific, a gross comparison of catch rates between the two oceans can be made. Catch and effort data given by the Japanese for Japanese longline operations in the Atlantic and eastern Pacific Oceans and plotted by Gottschalk (1972), show that the total effort in hooks fished was only slightly greater in the Atlantic than in the eastern Pacific for the period 1962 through 1970 (478×10^6 for the Atlantic and 442×10^6 for the eastern Pacific). Charts outlining longlining areas for striped marlin and sailfish in the eastern Pacific by Joseph et al (1973) and for sailfish and white marlin in the Atlantic by Wise and Davis[4] show that these areas are near equal in geographical extent. However, the catch-per-unit-effort (catch/hook) for striped marlin in the eastern Pacific has remained about three times greater over the years than the catch-per-unit-effort for white marlin in the Atlantic, a species that is similar in many respects to the striped marlin. The catch-per-unit-effort for sailfish in the eastern Pacific has averaged about four times the catch rate for the same species in the Atlantic.

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[4] Wise, John P. and Charles W. Davis. 1971. Seasonal distribution of billfish in the Atlantic. Prepared for 22nd Tuna Conference, NMFS, Miami, Fla., 28 p. (mimeo.).

These wide variations in catch rates between the Atlantic and eastern Pacific indicate a possibility of a lower density level or of a much smaller white marlin population, or both, in the Atlantic when compared with striped marlin in the eastern Pacific and sailfish in both oceans. If this is true, given approximately the same fishing effort, a greater percentage of tag recoveries of these species could be expected in the Atlantic.

The recovery rate of striped marlin tagged in the eastern Pacific using the FM-67 plastic tag was slightly less than for the metal tip tags used by the Woods Hole Oceanographic Institution Atlantic program for white marlin (1.06% eastern Pacific, 1.22% Atlantic). The plastic FT-1 tag gave near equal recovery rate results for sailfish in the Atlantic and the eastern Pacific (0.86% eastern Pacific, 0.80% Atlantic). The recovery rate for striped marlin tagged with metal tip "H" tags in the eastern Pacific has been 0.40%.

From the limited amount of data available, no definite conclusions can be reached. However, it appears that the plastic dart tag is as satisfactory as the metal tip dart tag. When the possible differences in population levels and projected recovery rates are considered, the plastic dart tag actually may prove to be superior.

In the northeastern Pacific there have been enough striped marlin tag recoveries to make some observations regarding their migration. Striped marlin usually are available during the first 3 months of the year off Mazatlán, Mexico. Movements of tagged fish from this area are toward the southwest and west, to and beyond the tip of Baja California. In late spring the principal component of the fishery changes to sailfish dominance.

Striped marlin are usually available about the tip of Baja California from late spring through fall. Migrations of tagged fish to the south and some to the west and northwest have been recorded. During late spring and early summer the reproductive activity of striped marlin increases in this area (M. Eldridge and P. Wares,[5] pers. comm.; Kume and Joseph, 1969). Thus the migrations away from the tip of Baja California in a southerly direction may be related to spawning activity of striped marlin in the general vicinity of the Revillagigedo Islands. Some spawning activity has been reported in this area by the Japanese longline fleet during the period late June through October (G. Adachi,[6] pers. comm.). Gonad indices for striped marlin collected in areas of reported spawning have been several times higher than the index found about the tip of Baja California (M. Eldridge,[5] pers. comm.).

Since the amount of longline fishing becomes less as one proceeds north of Magdalena Bay, Baja California, Mexico, the number of returns of striped marlin tagged about the tip and migrating northwest of the Magdalena Bay area would be reduced in proportion to the amount of fishing effort. However, some recoveries have been recorded northwest from the tip of Baja California toward southern California, immediately prior to the movement of striped marlin into the southern California fishery. An increase in catch per effort is noted in this area during the second and third quarters of the year. The southern California sport-fishery takes only a small number of striped marlin during late August through October (usually less than 500); the Japanese longline fleet does not operate in this area. Therefore the chance of recovering a striped marlin off southern California is remote. However, from the limited number of striped marlin tagged off southern California and recovered a short time later near the tip of Baja California, indications are that a southerly migration from southern California exists in the fall.

The rates of migration for striped marlin about the tip of Baja California-Mazatlán-Revillagigedo Island area was 1.9 nautical miles per day. Two westward records of long distance migrations from the coast of North America toward Hawaii show rates of 12.3 and 26.0 nautical miles per day. From southern California to near the tip of Baja California, four records show an average migration of 12.3 nautical miles per day. A southward migration from the tip of Baja California to near Clipperton Island was recorded at 16.3 nautical miles per day.

Distant water migrations from southern California and about the tip of Baja California show a much higher migration rate in nautical miles per day when compared with those recaptured near the tip of Baja California, Mexico.

Sailfish recoveries indicate little movement, the longest being 250 nautical miles. Figure 7 represents a summation of the major migrations of striped marlin in the eastern Pacific as determined by the cooperative tagging program. In general, recoveries of striped marlin in the eastern Pacific were short-term (89 days average) and the average migration distance was 281 nautical miles.

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Certain recommendations can be made regarding the future conduct of cooperative tagging programs in the Pacific for billfishes. These are as follows:

1. Encourage and develop billfish tagging (sport and commercial) throughout the entire Pacific for a better understanding of the migration patterns over the entire area for the major commercial and sport species. In the eastern and central Pacific additional tagging should be conducted off the Hawaiian Islands, southern California, Acapulco, Panama/Ecuador/Peru, Galapagos Islands, Tahiti, and Samoa.
2. Attempt to free-tag (harpoon method) or tag billfishes caught by non-injurious fishing techniques in sufficient numbers to determine hooking mortality.
3. Consider development of improved tags and tagging equipment and experimentally test both the metal tipped and plastic dart tags for histological compatibility and differential shedding by double-tagging billfishes or double-tagging large pelagic species in aquaria tests.
4. If additional tagging programs are to be undertaken in the Pacific in the future the programs should be coordinated between countries with regards to types of tags used, locations and seasons of tagging, publicity, recovery and reward procedures, to achieve the greatest return of information.

ACKNOWLEDGMENTS

Firstly, the success of the tagging program results from the interest and cooperation of the several thousands of billfish anglers who have actively participated by tagging and releasing their billfishes. Secondly, the cooperation of the managers of the various fishing resorts, charter boat skippers, and big game fishing clubs throughout the Pacific and the individuals allied with these organizations for they have been an important factor in the success of the program.

Individually, I would like to recognize Frank Mather III, Horace Witherspoon, William Craig, Gerald Talbot, Wally Giguere, Johanna Alban, and M. Eldridge for their interest and hard work on behalf of the cooperative tagging programs in the Pacific.

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EFFECTS OF BENZENE (A WATER-SOLUBLE COMPONENT OF CRUDE OIL) ON EGGS AND LARVAE OF PACIFIC HERRING AND NORTHERN ANCHOVY

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The effects of oil spills on the marine environment have received increasing attention over the past decade. A major portion of the research on these effects has followed a holistic approach of subjecting organisms to crude oil. Although these studies have contributed considerably to an understanding of the problem, oil is a complex amalgam of several components, varying in toxicity. It is difficult to ascertain specific effects on the survival and physiology of marine organisms using whole crude oil. While some studies have focused on the effect of tar components in oil (Bargmann, 1971; Moulder and Varley, 1971), little attention has been given to those compounds in crude oil thought most toxic to aquatic organisms, i.e., the low boiling point, water-soluble, aromatic hydrocarbons.

Most research to the present time at Tiburon Laboratory has concentrated on the effects of the aromatic component, benzene, on juvenile fishes (Brocksen and Bailey, 1973; Bailey and Brocksen, 1974; Benville and Korn, 1974; Korn and Macedo, 1974). Benzene is among the most abundant of the aromatic components, comprising at least 20% of the total aromatic hydrocarbons in crude oil. Benzene is relatively soluble in water (up to 2000 ppm in fresh water; Benville and Korn, 1974), and is among the most toxic of all oil components. Experiments are also in progress to test the effects of other toxic aromatics (toluene, xylene, 1, 2, 4-trimethylbenzene) on fishes, including synergistic and/or antagonistic effects of their combinations.

Since eggs and larvae are generally the life history stages most sensitive to environmental stress, and because few studies of the effects of oil components have been performed on these stages, experiments have been extended to test the effects of benzene on eggs and larvae of Pacific herring and northern anchovy.

The Pacific herring *(Clupea pallasi)* is an important commercial species in the San Francisco Bay area and along the coasts of Canada and Alaska (Eldridge and Kaill, 1973). In addition to a fishery for adults, there is a commercial fishery for the eggs which are principally exported to Japan. The eggs are demersal, being deposited on algae and substrate in bays from about October to March. Herring eggs and larvae occur inshore in bays where oil is likely to accumulate or be spilled.

The northern anchovy *(Engraulis mordax)* is the most abundant species with immediate harvest potential in the California Current System (Frey, 1971). It is also numerous in west coast bays where it has been found to be the most abundant fish, both numerically and in terms of biomass (Aplin, 1967). The anchovy spawns not only in San Francisco Bay but extensively throughout the California Current System of California (Ahlstrom, 1966). In offshore waters spawning occurs in every month of the year, usually peaking in late winter and early spring with another minor peak in early fall. In San Francisco Bay, however, spawning has been delimited from about May through October. Pelagic anchovy eggs are abundant in surface layers of San Francisco Bay and, like herring, they may possibly be exposed to oil.

This paper presents the results of preliminary experiments testing lethal and sublethal concentrations of benzene on eggs and larvae of the Pacific herring and northern anchovy. Developing embryos were exposed at two stages to contrast their sensitivity to benzene: (1) eggs a few hours after spawning and fertilization and (2) larvae a few hours before or after completion of yolk absorption. Parameters measured include percent mortality, percent abnormal larvae, types of abnormalities, length of larvae and growth, yolk utilization, feeding and respiration.

METHODS

Herring eggs were collected inshore on the Tiburon Peninsula a few hours after spawning occurred. Eggs, attached to intertidal algae (several species of *Fucus*, *Laminaria*, and *Gracilaria*) were in early cleavage stages when collected. Anchovy eggs were collected from Raccoon Straits between Tiburon Peninsula and Angel Island with a 0.5 meter plankton net (333μ mesh) towed on the surface. Although varying somewhat in developmental stage, most anchovy eggs were in gastrula stage when collected. Experiments performed on herring and anchovy eggs and larvae are summarized in Table 1.

After collection, eggs were sorted and placed into green polyethylene containers containing 8 liters of filtered seawater. Seawater was filtered through a series of two 5μ cellulose filters and one charcoal filter, removing most organisms and debris. To increase hatching, erythromycin gluceptate was added to a final concentration of 5 to 10 ppm. Rearing methods

TABLE 1

Summary of Conditions in Experiments Testing Effects of Benzene on Eggs and Larvae of Pacific Herring and Northern Anchovy. NM = Not Measured

Exp. No.	Date Begun	Day and Stage First Exposed	Mean Benzene Concentrations (ppm)	Total Exposure (Hrs)	Temp. (^oC)	Sal. (ppt)	Range and Mean			Food Spec. (No./ml)	Algae (No./ml)
							O_2 (ppm)	pH	NH_3 (ppm)		
Herring 1	2-05-73	Egg Day 0 Early Cleavage	0,3.8,16.5,39.1	24,48,96	14.0-17.5 (15.2)	(24.0)	NM	NM	NM	None	None
2	3-01-73	Egg Day 0 Early Cleavage	0,4.8,17.7,45.0	24,48,96	10.0-17.0 (13.2)	(24.0)	NM	NM	NM	5-10 *Artemia* nauplii	None
3	11-28-73	Larval Day 2	0,6.7,12.1	48	11.5-14.0 (12.9)	(22.0)	4.7-7.9 (7.0)	7.4-8.1 (7.9)	.011-.910 (.128)	9-20 (13) *Brachionus*	(10^5)
4	1-22-74	Larval Day 2	0,13.0,31.9	24,48	12.2-13.5 (12.9)	(10.0)	6.1-8.0 (7.3)	7.4-7.8 (7.6)	NM	4-9 (6) *Brachionus*	(10^5)
Anchovy 1	7-06-73	Day 0	0,0.4,2.7,7.5	24	17.5-19.2 (18.5)	(29.5)	7.1-8.0 (7.5)	7.7-7.9 (7.8)	.007-.030 (.014)	None	None
2	7-31-73	Day 0	0,4.7,10.5,24.0	24,48	16.5-18.0 (17.5)	(28.0)	7.0-8.0 (7.5)	7.6-7.8 (7.7)	.005-.040	None	None
3	8-14-73	Day 0	0,40.0	24,48	17.0-18.2 (17.5)	(28.0)	7.2-7.5 (7.4)	7.4-7.9 (7.6)	.010-.030	None	None
4	8-22-73	Day 0	0,13.5,19.5,53.5	24,48	16.8-18.4 (17.6)	(30.0)	(6.9-7.6) (7.3)	7.5-8.1 (7.9)	.010-.050	None	None

generally approximate those of Lasker *et al.* (1970) and Struhsaker *et al.* (1973).

All experiments were designed to permit multiway analysis of variance with two or more variables and three to five replicates per treatment combination. Replicate containers were placed randomly in water tables. In most experiments, 50 eggs were placed in each container. After sorting eggs into containers, various concentrations of benzene were added except for controls. On following days during development, benzene was added to give varying total exposure times of 0, 24, 48 and 96 hrs. Mean concentrations of benzene and exposure times are summarized in Table 1. After initial exposures, benzene concentrations declined over the 24-hr period due to volatization. For testing effects of 48- and 96-hr exposure times, additional benzene was added daily to achieve the initial concentration specified. The decline of three different initial benzene concentrations was measured every 2 hrs for 24 hrs under experimental conditions comparable to those in larval experiments. The decline in concentration is shown in Figure 1. The equation for the three calculated regression lines is $\underline{\hat{Y}} = ae^{-bX}$. The regression coefficients for each concentration (Fig. 1) were not significantly different ($P < 0.01$) (Sokol and Rohlf, 1969). After 24 hrs, 25% to 30% of the initial concentration remained for all three concentrations. All benzene concentrations were measured with a Model MT-220 Tracor gas chromatograph to the nearest 0.05 ppm (Benville and Korn, 1974).

Ranges and means of physical variables, algae and food concentrations are also given in Table 1. During initial experiments with herring (1 and 2), the controlled seawater system was not completed and a greater range of conditions prevailed. In all other experiments these variables were more closely controlled.

Herring eggs or larvae were subsampled daily from each treatment combination and examined for indications of abnormal rates and modes of development.

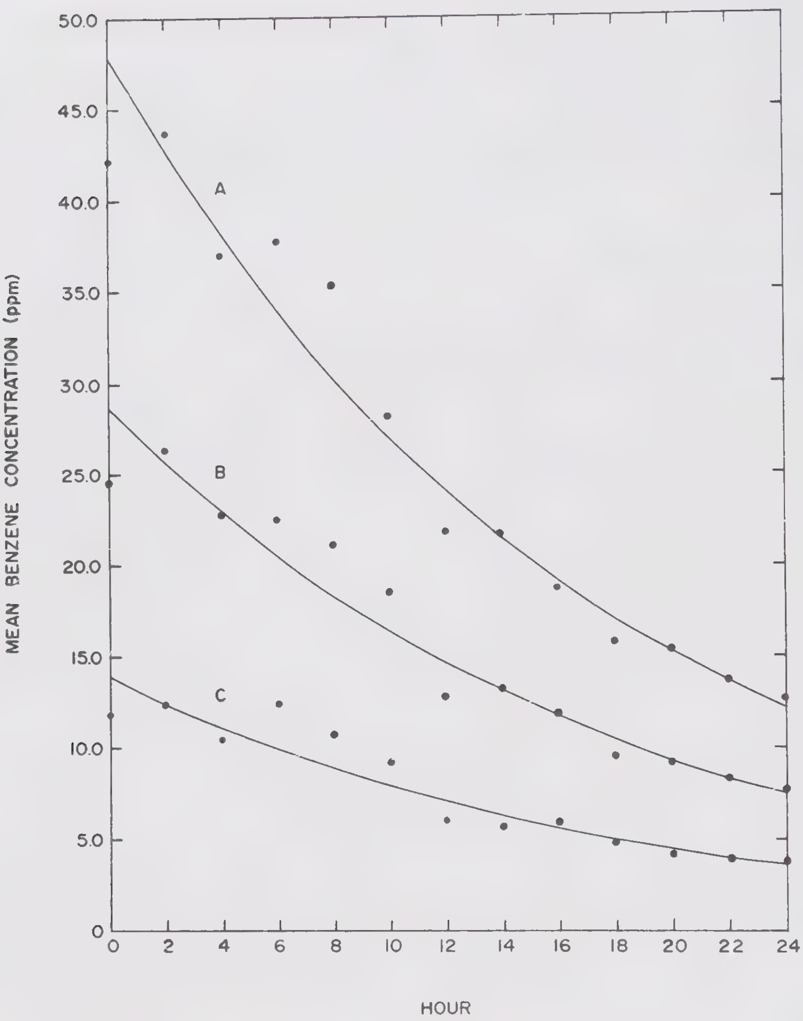

Fig. 1. Exponential decline in three initial benzene concentrations over a 24-hr period. Each point is the mean of three replicate containers. Range of temperature: 11.2°C-13.5°C. Equation for the calculated curve is: $\underline{\hat{Y}} = ae^{-bX}$
A-a = 47.8, b = .05697; B-a = 28.7, b = .05608; C-a = 13.9, b = .05648. All three regression coefficients were significant ($P < 0.01$)*. There was no significant difference between the three regression coefficients, (b) (Sokal and Rohlf, 1969).*

In some experiments, measurements of the standard length of larvae (most anterior point of snout to end of notochord) were made to the nearest 0.1 mm.

Herring larvae hatched in the laboratory after 9 to 11 days of incubation, while anchovy larvae hatched after 1 to 2 days of incubation. For herring, developmental days were designated as egg day or larval day depending upon experiment being discussed. Egg day 0 corresponds to the first 24 hrs after fertilization and larval day 0 to the day that larvae hatch. For anchovy, day 0 corresponds to the day of collection (gastrula) and egg and larval days are not separated since larvae hatch only 1 to 2 days after collection. At hatching, the following counts were made: number of actively swimming normal larvae, number of dead eggs remaining and number of abnormal larvae. Percent hatching and percent abnormal larvae among those hatching were calculated for each treatment combination.

In herring experiments 1 and 2 an attempt was made to feed larvae *Artemia salina* nauplii. Few larvae were able to feed (about 5%) because the nauplii were too large. In herring experiments 3 and 4, larvae were given rotifers *(Brachionus plicatilus)*, on which they fed readily. Culture methods for rotifers are given by Theilacker and McMaster (1971). *Nephroselmis* sp., isolated from San Francisco Bay, was added to cultures in the latter two experiments. Concentrations of food organisms and *Nephroselmis* are in Table 1. Counts of rotifers and *Nephroselmis* were made with a Model ZBI Coulter counter. In experiments exposing herring larvae, benzene was added on larval day 2, just after disappearance of the yolk sac. Daily counts from hatching to larval day 7 were made to determine percent survival.

Daily counts were not made in experiments with anchovy, because eggs and larvae were too small to be seen readily. Counts were made at the termination of the experiment and percent survival and abnormal larvae calculated. The standard length and size of yolk sac of surviving larvae were also measured at the end of the experiment. At the time of these experiments, rotifers had not been cultured and anchovy larvae were not fed. The experiments were ended prior to occurrence of starvation mortality (counted on days 3 or 6).

Larvae were observed for indications of abnormal swimming and feeding behavior. Also the percent of subsamples with food in guts was determined. All samples were preserved for more detailed studies of the effects of benzene on various morphometric characters.

Respiration of larvae was measured using a Gilson Respirometer. Ten larvae and 10 ml of seawater were placed in each 25 ml flask. Correction was applied from blanks containing only seawater.

Data were analyzed using the UCLA BMD computer programs 01V and 02V (Dixon, 1970).

RESULTS

HERRING

Exposed Eggs; Effect on Early Development and Hatching

After exposure of eggs to benzene, the developmental sequence appeared normal except at the higher concentrations (35-45 ppm range). In embryos treated with an initial mean concentration of 45.0 ppm, developmental rate was obviously delayed over that in controls. The heartbeat rate of normal embryos ranged from about 70 to 90 beats per minute. In embryos at 45.0 ppm the heartbeat rate was often irregular, sometimes increasing to 110 beats a minute, while at other times a few beats were missed altogether.

Hatching occurred from 9 to 11 days in the laboratory. At hatching, approximately 20% to 25% of the larvae appeared abnormal in all treatment combinations, including controls. Eggs from the same spawn collected in the field just prior to hatching also exhibited 20% to 25% abnormal larvae at hatching. Of these abnormal embryos, many simply did not develop and died before hatching. Others appeared to be retarded at an earlier stage of development, characterized by incomplete development of the body, fins and jaw. Yolk was not absorbed to the degree observed in normal larvae and the embryos remained dorsoventrally coiled over the yolk sac instead of straightening as in normal larvae at time of hatching. The high percent of abnormal, inviable larvae was observed among those hatching in all experiments with herring eggs collected from San Francisco Bay. In one experiment, using eggs from Tomales Bay, fewer abnormal larvae were observed. The possible reasons for this high percent of abnormal larvae at hatching are discussed below.

For brevity, and because data from the two experiments exposing eggs are comparable, only results from the second experiment (Table 1) are presented to illustrate the effects of benzene on eggs. The percent larvae hatching and percent of abnormal larvae at hatching are shown in Figure 2. Analysis of variance of the data showed a significant difference ($P < 0.01$) between concentrations, but not between exposure times. Significantly fewer larvae survived and significantly more larvae were abnormal at 45.0 ppm. Although the effects of different times of exposure were not significantly different, there is an indication that more larvae were abnormal at 48 hrs than at 24 and 96 hrs. At higher concentrations the time of exposure may have been more influential. The reason for the unusually high percent abnormal larvae at 17.7 ppm, 48 hrs is unclear. Most of these abnormal larvae occurred in only one replicate of the treatment combination and may be due to errors in application of benzene (too high concentration) added to the containers at the beginning of egg day 2. Other replicates at 17.7 ppm and 48 hrs were comparable to those at 24 and 96 hrs. Generally, it appears that herring eggs are relatively resistant to

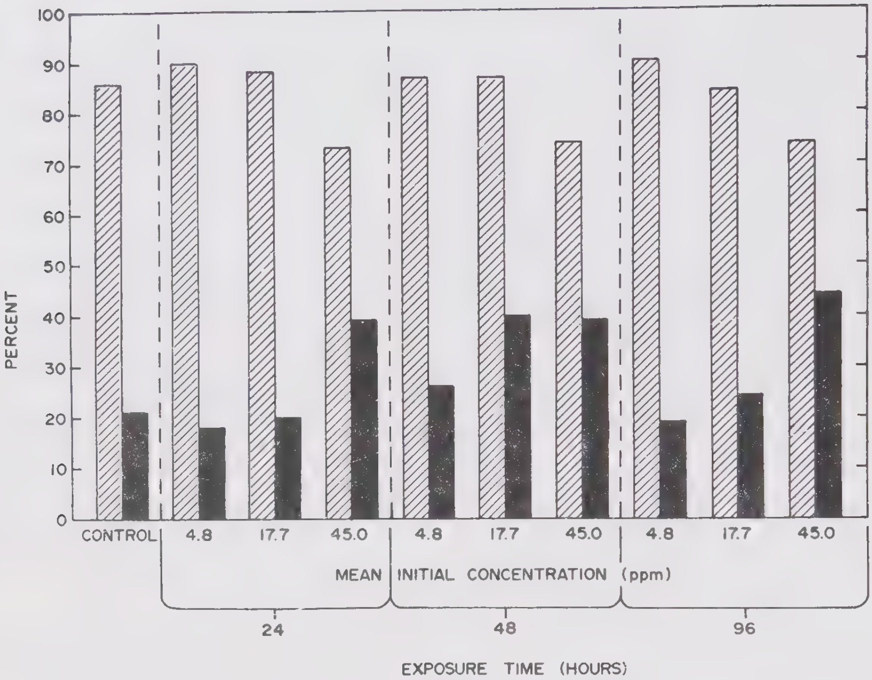

Fig. 2. Percent survival and percent abnormal among herring larvae at time of hatching after exposure of eggs to benzene. Herring experiment 2. Cross-hatched bars = percent survival, solid bars = percent abnormal.

benzene exposure. It should be remembered, however, that the benzene concentration declined over each 24-hr exposure period (Fig. 1). An initial concentration of 45 ppm is only 12 ppm or less after 24 hrs.

From the results of exposing herring eggs in experiment 1, it was noted that the 50% mortality level among larvae at time of hatching occurred at an initial mean concentration of approximately 40 to 45 ppm benzene when exposed for 96 hrs.

Among larvae exposed to a mean initial concentration of 45 ppm, all three exposure times, and larvae at 17.7 ppm, 96-hr exposure, abnormalities were observed that did not occur in controls and lower concentrations. Most common was some form of flexure along the body. Many larvae exhibited severe lateral or ventral bends just posterior to the head. Several were laterally bent to varying degrees of severity in the body and tail region; some both in the nape and tail region forming an s-shaped larva. A few had only one eye. Development of the lower jaw appeared incomplete. Of the abnormal larvae hatching, those most severely retarded or bent died shortly after hatching. A few of those less severely bent survived for several days, but were unable to swim or feed normally and eventually died.

Exposed Eggs; Survival of Larvae after Hatching

In herring experiment 2 (Table 1), an attempt was made to rear larvae past the period of yolk absorption by feeding larvae *Artemia salina* nauplii as reported by Talbot and Johnson (1972). The percent of larvae feeding and surviving daily for 33 days after hatching was recorded. It was observed that only a few larvae were feeding on the nauplii (5-10%), although these began feeding on larval day 1. The inability of most larvae to feed was probably due to the nauplii being too large. Yolk was absorbed by larval days 2 to 3 in all treatment combinations except at 45 ppm (approximately 1 day later). From larval days 1 to 7, survival of larvae at 4.8 ppm at all three exposure times was comparable to controls. In larvae at 17.7 ppm, 96 hrs, and 45 ppm, 48 and 96 hrs, survival was less than controls for these periods. This was due to the death of larvae with less obvious abnormalities. Starvation mortality began on about larval day 6 in all treatment combinations. Survival of feeding larvae was not significantly different between treatment combinations for the remainder of the experiment (33 days).

The standard length of surviving larvae (33 days from spawning) was measured and larvae of similar size from the field examined. Most major developmental characteristics were comparable. The standard length of laboratory larvae ranged from 12.4-17.0 mm; mean, 14.7 mm; there were two modal groups of 12.4-13.0 mm and 14.8-16.1 mm; most larvae were from 14.8-16.1 mm. There was no significant difference in standard length between larvae from different treatment combinations.

Larvae surviving for 33 days after higher benzene exposures of eggs appeared normal in all respects. At least some larvae are able to recover from all effects of the early exposure. However, at least 30% to 50% more larvae at 35 to 45 ppm benzene suffered irreversible effects leading ultimately to their death than did control larvae. The effects of benzene on exposed eggs are summarized in Table 2. Subsamples and surviving larvae were preserved and a more complete study of their morphometrics and abnormalities is underway and will be published separately.

Exposed Larvae; Effects on Feeding, Behavior, Development and Survival

Eggs were incubated for 9 to 11 days to obtain larvae for benzene exposure. Only normal larvae were used in experiments. Because brine shrimp nauplii were obviously inadequate food, larvae were given rotifers *(Brachionus plicatilus)* immediately after hatching. Larvae were observed feeding on rotifers on larval day 1. *Nephroselmis* were also added to provide food for rotifers. After completion of yolk absorption on larval day 2, benzene was added to containers (concentrations in Table 1). We chose to expose larvae at this stage in the assumption that they would be most sensitive to pollutant stress. Larvae reacted immediately to the benzene, swimming erratically and contracting violently. During the 7-day experimental period, the most obvious effect on larvae was on their swimming and feeding behavior. Many exposed larvae were lethargic, often lying on the bottom with reduced swimming and feeding movements, while controls were actively swimming or

TABLE 2

Summary of Effects of Benzene on Eggs and Larvae of Pacific Herring. Percents Are Approximate Estimates of the Significant Differences from Control Levels (P < 0.05). NS = Not Significant, LD = Larval Day

Stage Exposed	Approximate Concentration Range (ppm)	Exposure Time (Hrs)	Survival Hatching LD 0	Survival Larvae LD 3	Abnormal Larvae Hatching	Mean % Feeding LD 1-7	Respiration Rate	Stand. Length LD 1-7	Developmental Rate
Egg Day 0	3- 5	24	NS	NS	NS	---	---	---	NS
	15-20		NS	NS	NS	---	---	---	NS
	35-45		-15%	-10%	+20%	---	---	---	Delayed
Egg Day 0,1	3- 5	48	NS	NS	NS	---	---	---	NS
	15-20		NS	NS	NS	---	---	---	NS
	35-45		-15%	-10%	+20%	---	---	---	Delayed
Egg Day 0,1,2,3	3- 5	96	NS	NS	NS	---	---	---	NS
	15-20		NS	-10%	NS	---	---	---	Delayed
	35-45		-15%	-10%	+25%	---	---	---	Delayed
				LD 7					
Larval Day 2	5-10	24	Not exp. until LD 2	NS		---	---	NS	NS
	10-15			-10%		-25%	+25%	NS	Delayed
	30-35			-25%		-30%	+45%	NS	Delayed
Larval Day 2,3	5-10	48		NS		-25%	---	Smaller	Accelerated
	10-15			NS		-25%	---	Smaller	Delayed
	30-35			-70%		-50%	---	Smaller	Delayed

suspended in the water column and feeding normally. This lethargic behavior was most notable during the first 1 to 2 days after exposure. Subsequently, surviving larvae recovered, exhibiting normal swimming and feeding behavior. Their ability to recover and feed is shown by the percent of larvae with food observed in the gut (Table 3) over the 7-day period.

TABLE 3
Percent of Herring Larvae Subsample with Food (Rotifers) in Gut. Total Benzene Exposure of 48 Hrs, LD 0 and 1. Experiment 3

Concentration (ppm)	Larval Day								Mean (%)
	0	1	2	3	4	5	6	7	
0 - control		100	100	100	100	100	100	100	100
6.7		45	40	100	85	85	85	85	75
12.1		35	50	65	65	100	100	100	74

Unlike larvae hatching from exposed eggs, exposed larvae showed few obvious morphological abnormalities. Most notable was the delay in development. The developmental sequence appeared unaltered, but the treated larvae were approximately 1 day behind control larvae in rate of development. While most exposed larvae regained ability to feed, some appeared to feed rarely and subsequently the foregut and hindgut collapsed. After this occurred, no further feeding took place and larvae died. This was particularly noticeable in larvae exposed to higher concentrations of benzene (above 10 ppm). All larvae were preserved for further study of their morphometrics and abnormalities.

Figure 3 shows percent survival of larvae on day 7, 48-hr exposure of 6.7 and 12.1 ppm benzene (herring experiment 3). Analysis of variance of the data shows a significant difference between concentrations ($P < 0.05$). Significantly fewer larvae survived in 12.1 ppm than in controls. Apparently, larvae exposed to 6.7 ppm for 48 hrs were able to recover sufficiently to survive through the critical period of yolk absorption. Most remaining larvae from all treatments survived beyond larval day 7 without further significant mortality for 21 days.

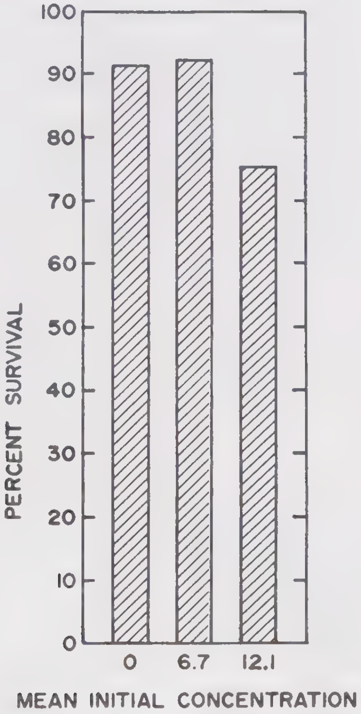

Fig. 3. Percent survival of herring larvae on larval day 7 after 48-hr exposure on larval day 2 and 3 to different concentrations of benzene. Herring experiment 3.

Figure 4 shows percent survival of larvae on the larval day preceding starvation mortality (herring experiment 4). The density of rotifers was inadequate to sustain normal growth and survival in this experiment (see Table 1). Significant differences in survival between treatments were found ($P < 0.05$). There was a significant difference between both concentrations and times of exposure. Fewer larvae survived at either concentration of benzene than in controls. Significantly fewer larvae survived at 48 hrs than at 24 hrs.

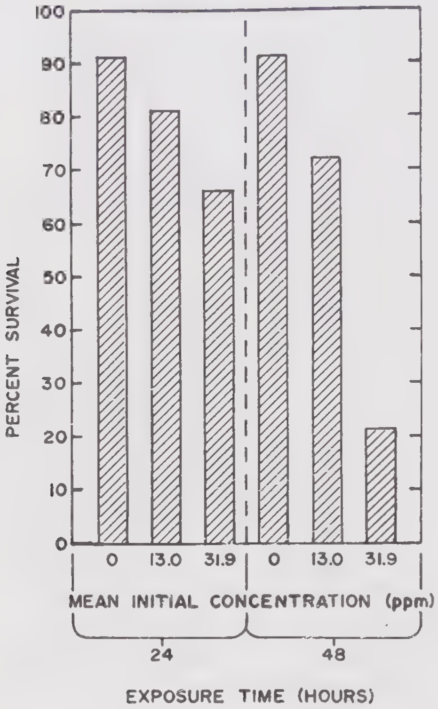

Fig. 4. Percent survival of herring larvae on larval day preceding starvation mortality after exposure to benzene on larval day 2 and/or 3. Herring experiment 4.

The 50% mortality level on larval day 7 is approximately a mean initial concentration of benzene of 20 to 25 ppm for 48 hrs exposure. Larvae seem to be more sensitive to lower concentrations of benzene than are eggs. Larvae, however, have the capacity to recover to some degree from the exposure while the affected embryos in eggs undergo irreversible effects.

Exposed Larvae; Effect on Growth and Respiration

Although many larvae treated with higher concentrations showed reduced feeding and delayed development, many were able to recover. Table 4 shows the mean standard length of larvae sampled on larval day 8 at the end of the experiment. Exposed larvae were significantly smaller than control larvae ($P < 0.05$). A difference of approximately 1.0 mm suggests that larval growth was retarded by benzene. In the future, measurements will be taken for a longer period to determine if exposed larvae are able to recover and attain size of control larvae.

Larvae exposed to benzene were placed in respiration flasks in the Gilson respirometer on larval day 3, 24 hrs after initial exposure. The total amount of oxygen consumed over a 24-hr period was recorded (Table 5). The results are preliminary, but show a significant increase ($P < 0.05$) in respiration exposed larvae over that of controls. Additional experiments are being performed on eggs and larvae of different developmental stages. The oxygen consumption is being measured at shorter 3-hr intervals for a total period of 24 hrs.

A summary of results of exposure of herring larvae is in Table 2.

TABLE 4

Mean Standard Length of Surviving Larvae (Day 8). Total Exposure of 48 Hrs. Experiment 3

Concentration (ppm)	Exposure Time (hrs)	Mean Standard Length (mm)	N
0 - control	---	10.3	80
6.7	48	9.4	80
12.1	48	9.2	80

TABLE 5

Summary of Preliminary Experiment Measuring Respiration in Herring Larvae (Larval Day 3) Exposed to Benzene for 24 Hrs. Larvae Acclimated for 30 Min Before Test. Test Run for 24 Hrs

Mean Concentration Benzene	Flask Number	Number Larvae	Oxygen Consumed in 24 Hrs Microliters/Larva	
0 - control	1	10	7.5	
	2	10	6.9	
	3	10	7.7	
	4	Malfunction		
Mean				7.4
13.0 ppm	1	10	8.0	
	2	10	9.7	
	3	10	12.3	
	4	9	10.4	
Mean				10.1
39.1 ppm	1	10	13.2	
	2	10	13.6	
	3	10	15.0	
	4	10	10.5	
Mean				13.1

A significant difference exists between all three treatments ($P < 0.05$).

ANCHOVY

Exposed Eggs and Larvae: Effect on Development and Survival

The effect of benzene on anchovy eggs and larvae was tested by exposing both stages in each experiment. Four experiments were done (Table 1). The first experiment exposed eggs to a single 24-hr exposure; the latter three studies included both 24- and 48-hr exposures. At the time of the experiments, rotifers had not been cultured and larvae were not fed. Survival of larvae on days 3 and 6 was determined. Because eggs at time of collection varied in developmental stage, the results of anchovy experiments are more variable than those for herring.

Figure 5 shows percent survival of anchovy larvae on days 3 and 6 for different mean initial

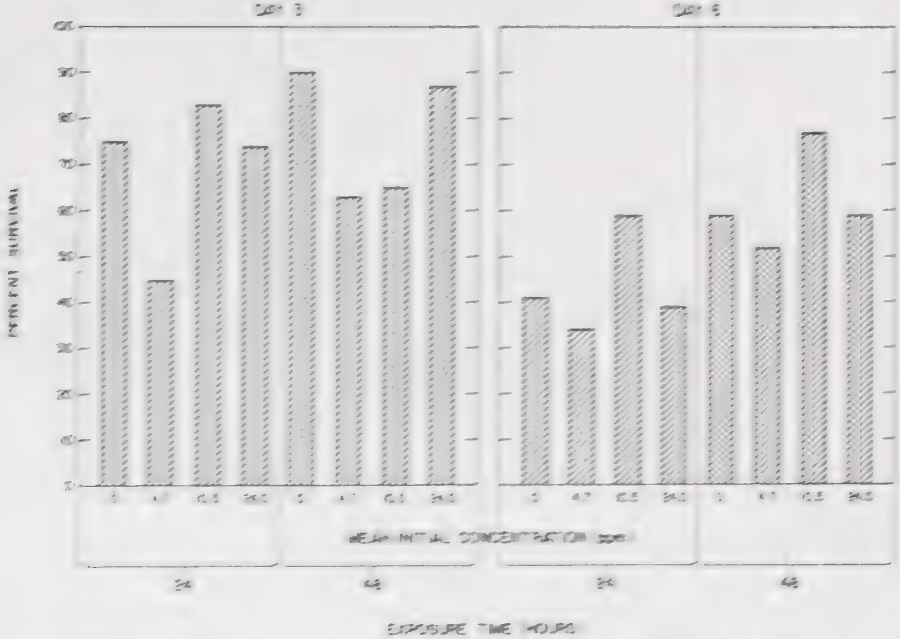

Fig. 5. Percent survival of anchovy larvae on days 3 and 6 after exposure of eggs and larvae to benzene. Anchovy experiment 2.

concentrations and exposure times. Refer to Figure 1 for actual concentrations over the 24-hr exposure period. On day 3, 24-hr exposure, survival of larvae was significantly lower ($P < 0.05$) at 4.7 ppm than in other concentrations and controls. Development at this concentration was accelerated over controls, whereas development at the higher concentrations was delayed (Table 6). On day 3, 48-hr exposure, an indication of lower survival is shown for larvae at 4.7 and 10.5 ppm. The difference, however, is not significant. On day 6, both 24- and 48-hr exposure, the pattern of larval survival was similar to that for day 3, 24 hrs, but differences were not significant. Except for larvae at 10.5 ppm, 48 hrs, on day 3, the same survival pattern persists throughout. There appears to be an acceleration of development and decreased survival at 4.7 ppm and delayed development and increased survival at 10.5 and 24.0 ppm. Larvae died earlier at 4.7 ppm, while at higher concentrations death of larvae was probably delayed due to narcotization. The slightly lower survival of larvae at 24.0 ppm was due to increased mortality of grossly abnormal larvae not occurring in other treatments. For both days, larval survival was significantly higher at 48 hrs because of delayed development. Additional experiments are planned to determine effects later in larval development when larvae are fed.

Figure 6 shows percent survival of anchovy larvae on day 6 for a concentration range overlapping that shown in Figure 5. When the two figures are compared on day 6, similarities are seen. Mean initial concentrations of 10.5, 13.5, 19.5 and 24 ppm show survival comparable to, or higher than, controls because of delayed development and mortality. At 53.5 ppm, however, survival is significantly less ($P < 0.05$) than controls and other treatments. Many abnormal larvae died at this concentration and, among those surviving (34%), approximately 30% were still abnormal in some way. Development of the surviving larvae (in 53.5 ppm) was greatly delayed over that of controls and they were also inactive. Even when fed

TABLE 6

Summary of Effects of Benzene on Eggs and Larvae of Northern Anchovy. Approximate Estimates of the Differences from Control Levels ($P < 0.05$) Derived from the Combination of All Experiments. NS = Not Significant

Stage Exposed	Approximate Concentration Range (ppm)	Exposure Time (hrs)	Larval Survival		Abnormal Larvae		Yolk Utilization	Standard Length		Developmental Rate	
			Day 3	Day 6	Day 3	Day 6	Day 3	Day 3	Day 6	Day 3	Day 6
Day 0 Egg	4- 5	24	-10%	NS	+25%	+20%	Accelerated	NS	NS	Accelera.	Accelera.
	5-10		NS	NS	+20%	+20%	Accelerated	NS	NS	Accelera.	Accelera.
	10-15		NS	NS	NS	+25%	Accelerated	NS	NS	Accelera.	Accelera.
	20-25		NS	NS	NS	+20%	Delayed	NS	NS	Delayed	Delayed
	40-55		NS	NS	+20%	+20%	Delayed	Smaller	Smaller	Delayed	Delayed
Day 0 Day 1 Egg and Larva	4- 5	48	-10%	NS	+20%	NS*	Accelerated	NS	Larger	Accelera.	Delayed
	5-10		-10%	NS	+20%	NS*	Delayed	NS	Larger	Delayed	Delayed
	10-15		-10%	NS	+25%	NS*	Delayed	NS	Larger	Delayed	Delayed
	20-25		NS	NS	+50%	NS*	Delayed	NS	Larger	Delayed	Delayed
	40-55		NS	-15%	+50%	+30%*	Delayed	Smaller	Smaller	Delayed	Delayed

*Most abnormal larvae died by day 6, thus no significant difference from control as in day 3.

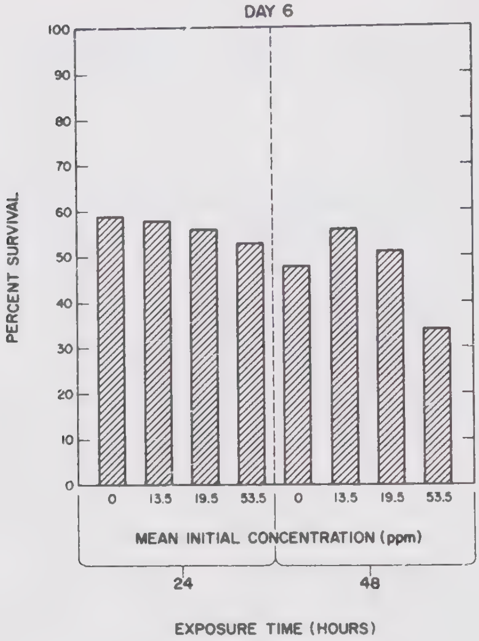

Fig. 6. Percent survival of anchovy larvae on day 6 after exposure of eggs and larvae to benzene. Anchovy experiment 4.

they would die a few days later. Assuming these abnormal larvae will die, the lowest mean initial concentration range at which 50% mortality occurs is approximately 20 to 25 ppm.

Figure 7 shows percent abnormal larvae among those surviving on days 3 and 6 for the same experiment as in Figure 5. On day 3, 24- and 48-hr exposure, there was a significant difference ($P < 0.05$) between controls and exposed larvae. On day 3, 48 hrs, there were significantly ($P < 0.05$) more abnormal larvae at 24 ppm than controls and other treatments. On day 6, there were fewer abnormal larvae among survivors than on day 3, because most grossly abnormal larvae had already died. The only significant difference in percent abnormal larvae on day 6 was between controls and larvae exposed to 24 ppm, 48 hrs ($P < 0.05$).

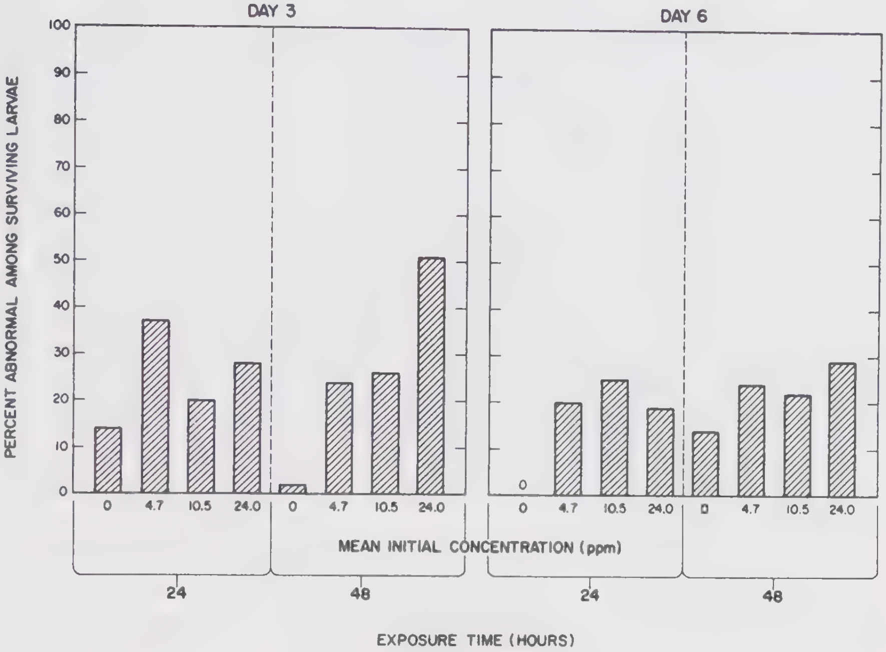

Fig. 7. Percent of abnormal anchovy larvae among larvae surviving to days 3 and 6 after exposure of eggs and larvae to benzene. Anchovy experiment 2.

The development of embryos before hatching was not observed in these experiments. When the experiment was ended, control larvae were examined and compared to larvae at approximately the same stage collected from the bay. No obvious differences were observed. Anchovy larvae treated with benzene exhibited abnormalities similar to those described earlier for herring larvae, the most obvious being bending of the notochord and somatic musculature ("bent larvae"). They were preserved for study of their morphometrics and abnormalities.

Unlike herring, few anchovy larvae were abnormal in the controls. The maximum percent of abnormal larvae observed in any experiment was from 10% to 15%. These abnormalities were not severe and usually occurred either when eggs were not treated with antibiotics before hatching or in eggs spawned later in the spawning season.

Benzene affected the developmental rates of the exposed eggs and larvae. Figure 8 shows the percent of larvae with yolk remaining on day 3 after 24-hr exposure of the egg. This illustrates the accelerated utilization of yolk at lower concentrations. Up to 10 ppm the differences from controls are significant ($P < 0.05$). Utilization of yolk at 24 ppm and, in other experiments, at 40 to 55 ppm is delayed. A difference in rate of yolk utilization occurs in larvae at concentrations of 4.7 and 10.5 ppm depending upon the length of exposure. When exposed for only 24 hrs, yolk is utilized more rapidly in both these concentrations than in controls. When exposed for 48 hrs, yolk utilization is delayed at both concentrations (see Table 6).

This pattern of yolk absorption is also reflected in the mean standard length of larvae on day 3 (Fig. 9). Differences in mean standard length are

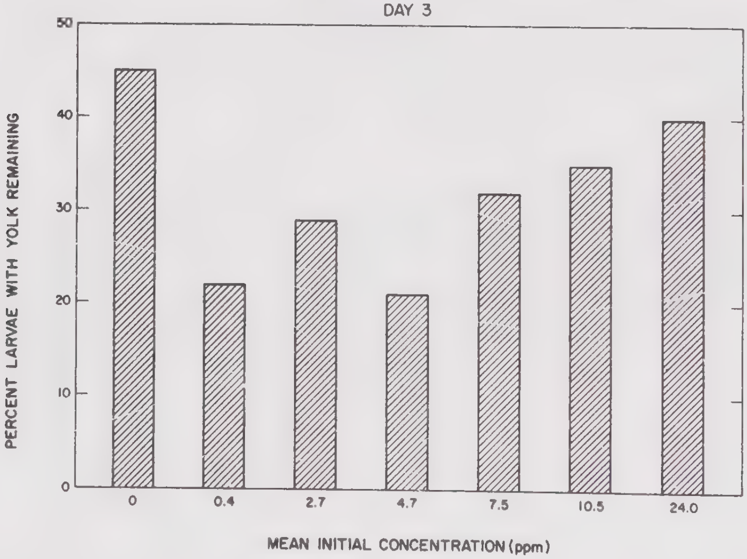

Fig. 8. Percent of larval anchovies with yolk remaining on day 3 after exposure of eggs for 24 hrs to different concentrations of benzene. Anchovy experiments 1 and 2.

not significant between concentrations or exposure times on day 3. On day 6, however, there are significant differences (P < 0.01) in the size of larvae correlated with developmental rate and yolk absorption. Control larvae decreased in size from day 3 to day 6. They were active, but not fed, and thus resorbed tissue. When eggs were exposed for 24 hrs to 4.7 ppm, larvae on day 6 were larger than in controls, but smaller than those in 10.5 ppm. They utilized yolk more rapidly, but size remained about the same as day 3. Even though more active than larvae at higher concentrations, they were not as active as control larvae and resorbed less tissue. When eggs were exposed for 24 hrs to 10.5 ppm, larvae

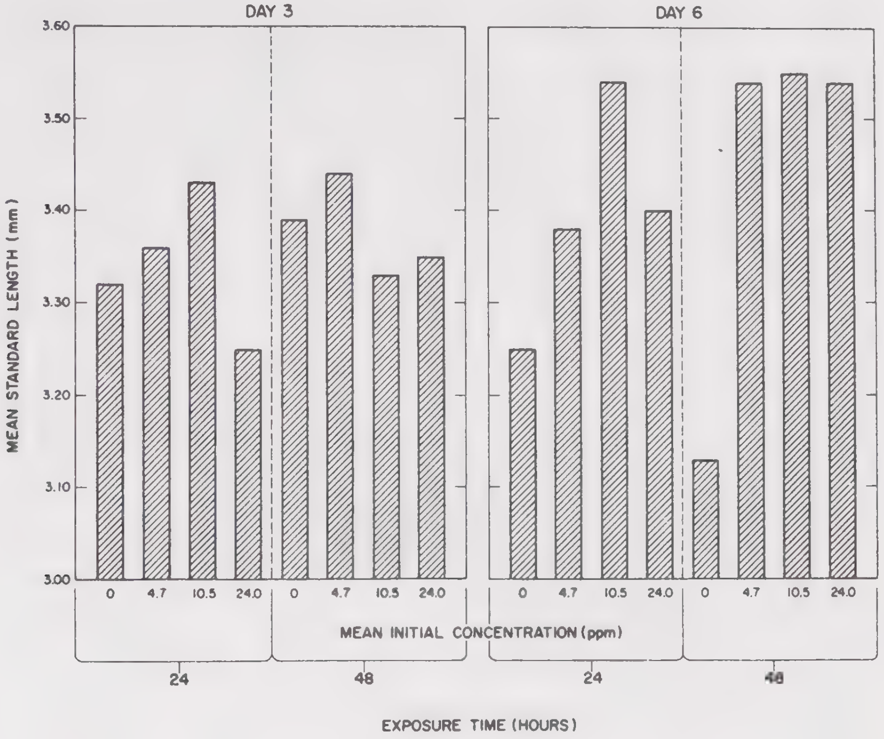

Fig. 9. Mean standard length of anchovy larvae on days 3 and 6 after exposure of eggs and larvae to benzene. Anchovy experiment 2.

on day 6 were larger than in other treatments. They were probably narcotized and absorbed yolk more slowly. Because the larvae were less active, energy derived from yolk was channeled into growth. Resorption of tissue would probably occur later. When eggs were exposed for 24 hrs to 24 ppm, larvae on day 6 were larger than controls because of slower yolk absorption and development. Larvae at 24 ppm were less in mean standard length than those at 10.5 ppm because smaller, abnormal larvae were included in the measurements.

When eggs and larvae were exposed for 48 hrs, by day 6 all exposed larvae were larger than controls. Only normal larvae in all treatments were measured. At all concentrations, development was delayed and larvae were relatively inactive. Most energy derived from yolk absorption was expended in growth and tissue was not resorbed through activity as in control larvae. Whether the exposed larvae are able to recover later in development as did herring larvae is not known. Experiments are planned for next spawning season in which larvae will be fed and the delayed effects examined.

DISCUSSION

Benzene induces considerable physiological stress on eggs and larvae of herring and anchovy over much of the initial concentration range tested (approximately 5 to 50 ppm). Both lethal and sublethal effects were noted in measurements of survival and other parameters indicative of metabolic rate. The lethal effects of benzene are summarized in Table 7 as 50% mortality levels at certain stages. Because benzene volatilizes, calculated concentrations are given for various times. Maintenance of a constant concentration of benzene in an open system, such as that used in tests with juveniles and adults (Benville and Korn, 1974), was not possible. When a constant concentration is maintained, a fungus-like organism, apparently

TABLE 7

Summary of Concentrations and Exposure Times of Benzene Causing 50% Mortality in Herring and Anchovy Eggs and Larvae

Species	Stage Exposed	Stage 50% Mortality	Approximate Calculated Concentrations Over 24 Hrs* Initial	6	12	18	24	Initial Conc. Range (ppm)	Exposure Time (Hrs)
Herring	Eggs	At Hatching	40	29	20	15	10	40-45	96
			45	32	23	16	12		
Herring	Larval Day 2	Larval Day 7	20	14	10	7	5	20-25	48
			25	18	13	9	7		
Anchovy	Egg and Larval Day 1	Larval Day 3	20	14	10	7	5	20-25	48
			25	18	13	9	7		

*Calculated from the equation $\underline{\hat{Y}} = ae^{-.0565X}$ (refer to Fig. 1).

using benzene as an energy source, grows over the chorionic surface and the eggs die. We are trying to identify this organism and attempting to define its growth requirements as well as means of eliminating it from laboratory cultures.

A single exposure of benzene may approximate what occurs in the field. The initial benzene put into solution in the field undoubtedly volatilizes and the concentration declines over time. We plan to conduct spatial and temporal sampling in San Francisco Bay in order to determine actual concentrations of benzene and other aromatic components in the water column, both in areas of chronic oil pollution and in the event of a spill. Benzene may interact synergistically with other water-soluble aromatic components to produce greater effects than that of benzene alone. Data on concentrations of aromatics in either estuaries or oceans, however, are incomplete.

Sublethal effects of benzene on yolk absorption, growth and respiration show that benzene influences metabolic rate and energy utilization of embryos and larvae. At lower concentrations, metabolic rate is accelerated with a resultant energy cost in the alleviation of stress. At higher concentrations, metabolic rate is delayed, probably because larvae are narcotized. We plan to do additional measurements of respiration and growth to determine effects of the aromatic components on the energy budget of the larvae.

Reference to Table 7 shows that a greater exposure of benzene is required to affect mortality in exposed eggs than in exposed larvae. The exposure of eggs, however, induces abnormalities in the embryos. The effect is permanent, larvae eventually dying. It is interesting that many exposed herring and anchovy larvae are able to recover even though they undergo temporary effects. Those that survive 3 days after the last exposure often recover all feeding and swimming activity. There may be, however, delayed effects in development and growth not obvious until later in larval development. Herring and anchovy larvae showed

50% mortality at approximately the same concentration range of 20 to 25 ppm (Table 7).

Brocksen and Bailey (1973) found similar effects of benzene on the metabolic rate of juvenile striped bass and chinook salmon, evaluated by measuring their respiration rate at different concentrations and exposure times. They found an increase in respiration at lower concentrations and shorter exposure times. In contrast, at higher concentrations and longer exposures, narcotization occurred and respiration was reduced. They also found that fish recovered from exposures. Brocksen and Bailey (1973) provide an explanation of the possible biochemical pathways involved in benzene metabolism which may account for these effects on respiration.

Most other studies of the effect of oil on larval fish have been with whole crude oil or crude oil fractions. Kühnhold (1969, 1970) has tested the effect of several crude oils and their water-soluble fractions on Atlantic herring *(Clupea harengus)* larvae. At the National Marine Fisheries Service laboratory at Auke Bay, Alaska, the effect of water-soluble fractions of Prudhoe Bay crude oil was tested on Pacific herring *(C. pallasi)* and pink salmon fry *(Oncorhynchus gorbuscha)* (Stanley Rice, personal communication). Since we are studying the isolated physiological effects of benzene, our results cannot be legitimately compared.

It is probable that oil, acting synergistically with other pollutants such as pesticides deleteriously affects the young stages of fish and invertebrates in polluted estuaries. Many of these fish and invertebrates are important sport and commercial fisheries resources. Although the decline in their populations cannot be attributed solely to the effects of oil, oil and other pollutants may act together in significantly reducing larval recruitment in estuarine-dependent species.

The higher percent of abnormal larvae observed in larval herring hatching from eggs spawned in

San Francisco Bay than in the relatively unpolluted waters of Tomales Bay farther north may indicate that San Francisco Bay water is already polluted sufficiently to stress eggs after spawning. Although some genetic variation in viability could be expected in species producing such large numbers of eggs, it is unlikely that 20% to 25% would be genetically inviable. Abnormal eggs may also result from deleterious effects of pollutants on the development of eggs in gonads of adults. Since aromatics are highly soluble in lipid tissues, such as eggs, we plan to study this problem further.

The applied benefit of this research is obvious in view of the increasing possibility of oil spills, blowouts, effluents, and ballast dumping in the future. Recommendations on allowable levels of oil must involve knowledge of specific effects at sublethal concentrations as well as immediate lethal effects.

ACKNOWLEDGMENTS

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PAPER 1095

epwater Shrimp Trapping in Hawaiian Islands

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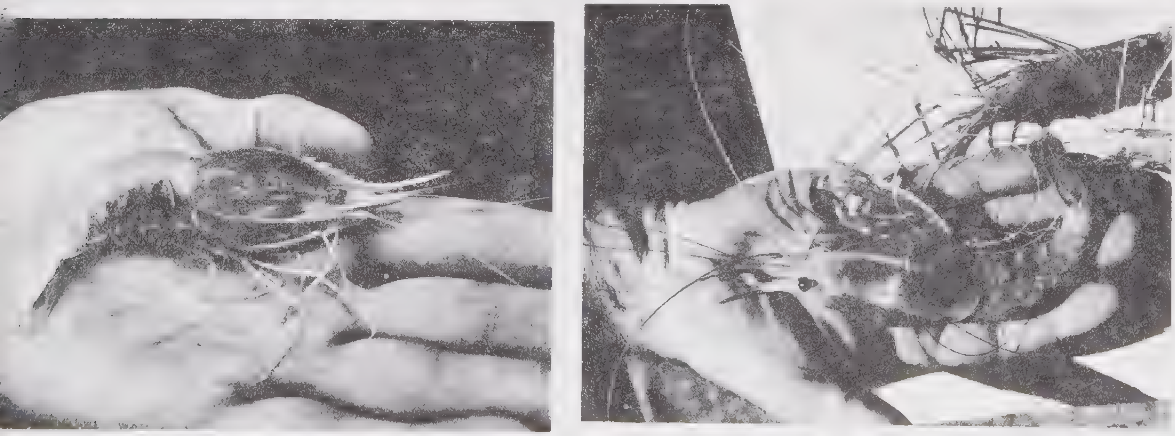
STRACT—The results of preliminary deepwater shrimp trapping sur- i in the Hawaiian Islands consisting of 82 sets involving totals of 306 and 3,960 h of fishing time in the 75 to 450-fathom (135-825 m) h range are discussed. A variety of traps, bait containers, and baits tested. Attempts to capture the penaeid shrimp, Penaeus marginatus, *bstantial numbers were unsuccessful. More success was experienced apping the caridean shrimps* Heterocarpus ensifer *and* H. laevigatus. *hese species, it was found that traps covered with burlap cloth out- d uncovered traps by factors of 2.5 to 10.* H. ensifer *was found to be abundant in depths of 200-250 fathoms (365-455 m) where catches optimum trap and bait combinations ranged from 15 to 63 pounds (6.8 3.6 kg) per trap for sets of less than 24 h duration. Seventy traps set night during spring 1973 off the south coast of Oahu produced a total 015 pounds (460 kg) for an average of 14.5 pounds (6.6 kg) per trap. larger* H. laevigatus *was found to be most abundant in depths of 375 fathoms (440-685 m), where catches ranged up to 34.8 pounds kg) for 4 traps. It is speculated that the various species of* Heterocar- *represent an unexploited world resource of considerable magnitude.*

RODUCTION

uring 1967 and 1968 the National ie Fisheries Service (NMFS) de- four cruises of the RV *Town- Cromwell* to demersal resource ys in the Hawaiian Islands. The ry sampling gear utilized were p trawls, although a few shrimp tations were effected. These sur- demonstrated that the penaeid p, *Penaeus marginatus* Randall, available in modest amounts and amenable to harvest by shrimp trawls in depths of 60-125 fathoms (110-230 m)[1] (Yoshida, 1972; Struhsaker, Yoshida, and Shomura[2]). Two species of caridean shrimps, *Heterocarpus ensifer* Milne-Edwards and *H. laevigatus* Bate (Fig. 1), were also taken in moderate numbers with the trawls between 150 and 400 fathoms (275 and 730 m). However, the initial investigations indicated that trapping, rather than trawling, was perhaps a more effective method for capturing these latter species.

Clarke (1972) conducted trapping surveys during 1969 and 1970 at several locales off the Hawaiian island of Oahu. The sampling gear consisted of several trap types, but all were uncovered traps constructed of 0.5-inch (13-mm) mesh wire screens. This work provided data on the biology and depth distribution of *H. ensifer* and *H. laevigatus* and indicated that *H. ensifer* might be present in sufficient quantities to support a commercial fishery.

Further trapping trials were intermittently conducted by NMFS during 1971-73 at various localities in the Hawaiian Islands. These trials were of a preliminary nature, and various combinations of traps, bait containers, and baits were utilized. Most of the data were obtained during fall 1972 and it became apparent at this time that burlap-covered traps were more effective in capturing *H. ensifer* than were uncovered traps. Attempts to trap *P. marginatus* in substantial numbers were unsuccessful. Follow-up cruises with more extensive trapping



1.—A fresh specimen of *Heterocarpus ensifer* (A, left) about 115 mm total length. Note ocellus on the side of the cephalothorax ("head") and the backwardly projecting spines on the third and fourth segments of the abdomen ("tail"). A fresh specimen of *Heterocarpus laevigatus* (right, B) 175 mm total length.

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[1] Metric equivalents are approximate.

[2] Struhsaker, P., H.O. Yoshida, and R.S. Shomura, Exploratory shrimp trawling in the Hawaiian Islands, unpubl. ms., Southwest Fisheries Center, Honolulu Laboratory, Honolulu, HI 96812.

trials scheduled for 1973 were cancelled.

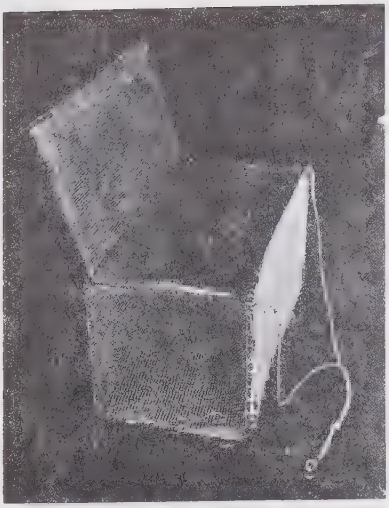


Figure 2.—A covered square trap. This trap type produced the best catches of *Heterocarpus ensifer*.

GEAR AND SAMPLING EFFORT

Gear

The "square trap" (in reference to its square cross-section) produced the best catches of *Heterocarpus*. It measures 2×2×4 feet (60×60×120 cm) (Fig. 2). The frame is constructed of ⅜-inch (10-mm) diameter steel bar and is enclosed with 0.5-inch square mesh galvanized wire screen. The sides, top, and bottom are then covered with burlap. The tunnels (one at each end) are also constructed with the screen (but are uncovered) and taper to approximately 3-inch (75-mm) diameter openings about one-third the distance in from each end. Covered and uncovered traps of similar construction, but enclosed with 1-inch (25-mm) (bar-to-bar) hexagonal wire screening were also tested.

"Flat traps" (Fig. 3), constructed similarly to the square traps, but measuring 1×2×4 feet (30×60×120 cm), were utilized most often in the shallower depths surveyed. It was felt that the lower ramp angles of the tunnels might prove to be more effective in capturing *P. marginatus*. Captive specimens of *P. marginatus* held in large tanks ashore tended to maintain close contact with the bottom and usually did not undergo exploratory swimming behavior off the bottom such as has been observed for Alaskan pandalid shrimps in the vicinity of traps (Kessler, 1969).

Collapsible round shrimp traps (Fig. 4) were also tested to a limited degree. They are 14 inches (36 cm) high, 24 inches (60 cm) in diameter at the top, 34 inches (86 cm) in diameter at the bottom and have shallow tunnels leading to four entrances. The webbing consists of 1.25-inch (31-mm) stretched mesh nylon.

Finally, an experimental collapsible "tent trap" (Figs. 5, 6, and 7) was tested on one occasion. Each of the three frames making up the bottom, side, and lid of the trap measures 2×4 feet (60×120 cm) and is enclosed with 0.5-inch wire mesh screen. The three frames are joined with split links of a size that permit folding of the frames and are covered with a single piece of burlap. A bridle attached to the corners of the lid runs through the outside corners of the bottom frame (Fig. 6). When closed, the lid is secured with a rubber strap and S-hooks. The triangular end frames are attached to the bottom of the trap by split links and have two half-links welded on the leg articulating with the side frame (Fig. 7). The tunnels are constructed with 1.5-inch (38-mm) mesh (stretched) nylon webbing and are secured to entrance rings 3 inches (75 mm) in diameter. The tunnels are held in place by a rubber strap and S-hook (Fig. 6).

Several bait containers were tested. Containers constructed of 0.5-inch mesh screen measuring about 4×4×6 inches (10×10×15 cm) were generally superior to plastic containers of the same size perforated with 0.25-inch (6-mm) holes or bait wrapped in cheese cloth. From 1 to 2 pounds (0.5-1 kg) of bait were sufficient for sets of 12-14 h. The bait containers were suspended near the center of the trap.

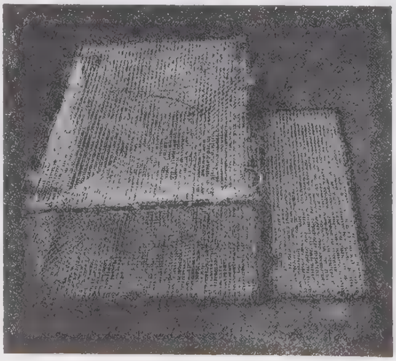


Figure 3.—An uncovered flat trap.

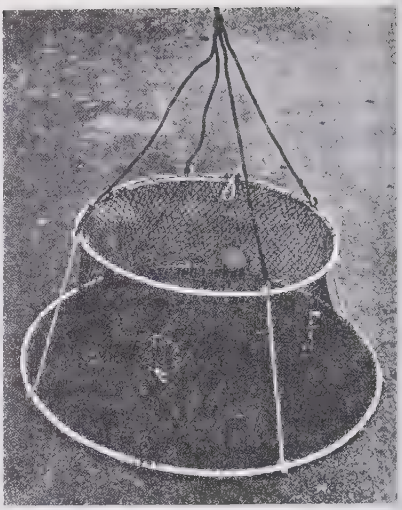


Figure 4.—A collapsible shrimp pot.

Each trap has a 7-foot (215-cm) bridle of 0.25-inch diameter polypropylene rope attached to two corners on the top of the trap. Although this results in considerable drag when hauling back the gear, it is felt that this arrangement may, in the case of square traps, eliminate the possibility of the trap landing on end when being set. It was also thought that this would reduce the number of shrimp washed out through the entrances when hauling back. The bridle has a snap at the center for attachment to the ground line. The ground line and buoy line consist of 0.5-inch polypropylene rope. The traps are spaced at 10-fathom (20-m) intervals, and the first and last traps on a string have 5- or 10-pound (2.3 or 4.5-kg) anchors attached by a short wire to a trap corner. We usually fished 4-6 traps to a string. Our buoy lines are made up into 100-fathom (185-m) lengths, and these are stored in plastic garbage containers of approximately 32-gallon (120-liter) capacity. This arrangement provides the flexibility required when conducting surveys encompassing a wide depth range.

The ground line is made by forming loops for each trap at 10-fathom intervals on the distal portion of the first 100-fathom section. The proper number of 100-fathom sections are then added as the traps are set in order to give an excess amount of buoy line

25-50 fathoms (45-90 m) below the end of the last section to assure that the polypropylene line does not float at the sea surface. The set is retrieved with a line-hauling power block; the 100-fathom sections are stowed directly into their containers as the line comes aboard.

Because of the buoyancy of the polypropylene line, minimal flotation for the marker buoy is required. Our buoys consisted of either simple bamboo poles with two or three plastic into a weighted frame which is floated with a large inner tube. These buoys remained at the surface even in areas where the currents approached 3 knots. A 4-fathom (7-m) pickup line with a small float is attached to the buoy.

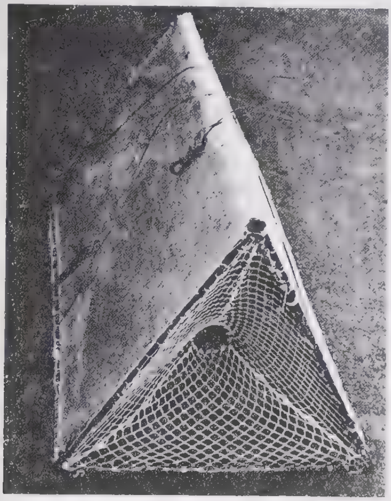


Figure 5.—A collapsible tent trap ready for fishing.

Distribution of Sampling Effort

From March 1971 to August 1973, 82 exploratory shrimp trapping sets involving totals of 306 traps and about 3,960 h of fishing time were effected in various areas of the Hawaiian Islands. The distribution of sampling effort by depth was as follows: 75-130 fathoms (135-235 m), 24 sets; 130-200 fathoms (235-365 m), 2 sets; 200-300 fathoms (365-550 m), 47 sets; 300-400 fathoms (550-730 m), 7 sets; 400-450 fathoms (730-825 m); 2 sets. Most sampling effort was expended in depths of 75-130 fathoms and 200-300 fathoms where *P. marginatus* and *H. ensifer*, respectively, are most abundant.

Most of the trapping effort for *P. marginatus* took place in the Pailolo Channel where this species is most abundant (Struhsaker et al., unpubl. ms.). The deeper depth ranges explored with the RV *Townsend Cromwell* were off the north coast of Oahu, the north edge of Penguin Bank, off our gear by personnel of the Hawaii Institute of Marine Biology (HIMB) utilizing the FV *Valiant Maid*. During August 1973, 9 sets were made with the RV *David Starr Jordon* in the Leeward Islands of the Hawaiian Archipelago near Necker Island, French Frigate Shoal, Laysan Island, and Pioneer Bank.

Because the trapping experiments were interspersed with other vessel activities, most sets were made at dusk and retrieved at dawn. However, we do have a few data for daytime sets. We trapped on a variety of bottom types, avoiding only steeply sloping areas and rough-bottom grounds where the traps might have been snagged.

RESULTS

Trapping for *Penaeus marginatus*

Attempts to trap *P. marginatus* in substantial numbers were unsuccessful, but the sampling effort was of a very preliminary nature. After generally negative results obtained during spring 1971, experiments with captive shrimp were conducted at the NMFS Kewalo Basin facility. Response of the shrimp was noted during hours of light and darkness to baited and unbaited flat traps (all uncovered) equip-

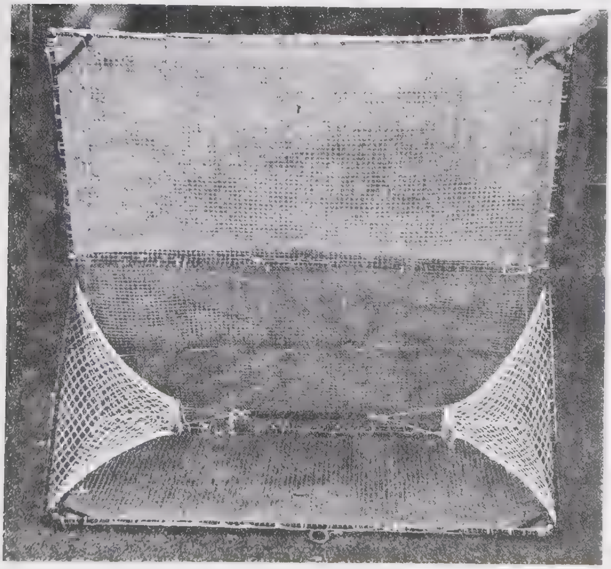
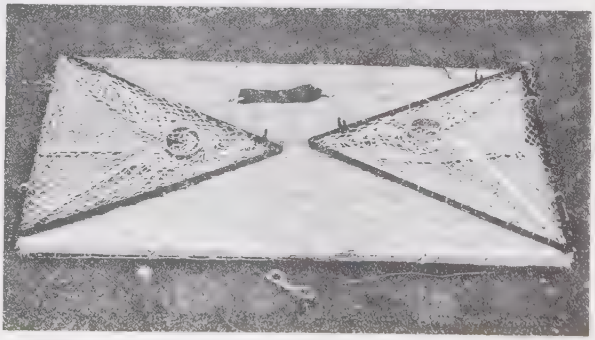


Figure 6.—A tent trap with raised lid.

Figure 7.—A collapsed tent trap. The end frames fold outward, over the bottom panel.



ped with a variety of entrances. Rather surprisingly, there were no major differences in the catch rates between the various combinations of the trap types and baits tested. These results were probably confused by abnormal temperature and light conditions. Although adult *P. marginatus* appear to be negatively phototactic (Struhsaker et al., unpubl. ms.), best capture results were obtained by suspending a light over an unbaited trap. This resulted in all of the available shrimp (18-20) in a test tank 24 feet (7 m) in diameter entering the trap within 15-20 minutes.

Further field trials conducted during fall 1972 were inconclusive, aside from determining that flat traps outfished square traps on the same string. Traps containing a deep-sea diving light captured shrimp on three occasions when the other traps on the string did not take any shrimp (maximum single trap catch, five shrimp). However, the best catch of nine shrimp for an overnight set was in an uncovered flat trap baited with finely ground fish. Three sets of traps fished during daylight hours produced low catches similar to night sets.

Clarke (1972) reported a best catch of this species as 26 individuals in eight traps in 60 fathoms (110 m) off the north coast of Oahu. We feel that concerted trapping trials for this species might result in a viable fishing strategy that could produce catches of commercial value for small vessels.

Trapping for *Heterocarpus ensifer*

During fall 1972 several types of traps, bait containers, and baits were tested in various combinations on sets of 4-6 traps per string. These preliminary trials were not designed for the results to be subjected to statistical evaluation, but the main trends of the effectiveness of the various trap combinations in capturing *H. ensifer* were readily apparent.

Square traps with 0.5-inch mesh wire screen were more effective than the other types tested. The catches of square traps with 1-inch mesh wire screen were less, apparently owing to escapement. Catches from the flat traps and round traps were consistently lower than for the square traps. The performance of burlap-covered and uncovered square traps with 0.5-inch mesh were directly compared on eight occasions when strings of alternating trap types were set. The covered traps always outfished the uncovered traps by factors of 2.5 to 10.

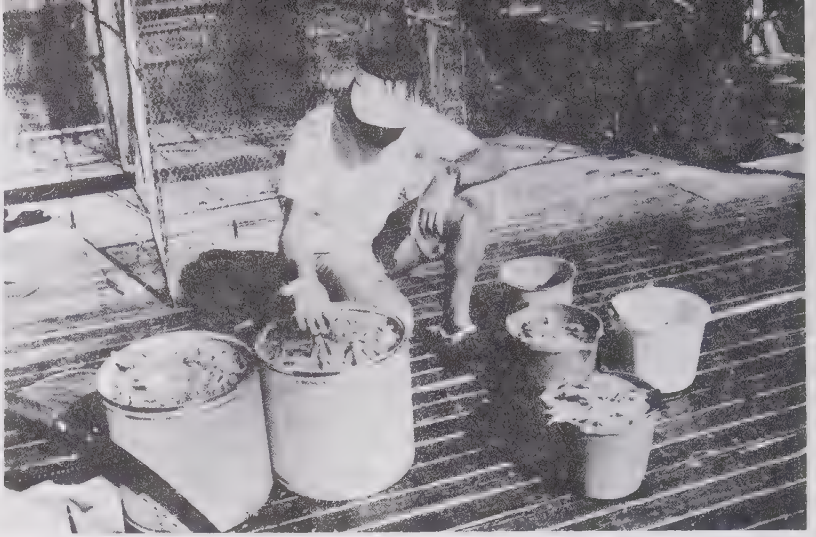


Figure 8.—A 123-pound (56-kg) catch of *Heterocarpus ensifer* produced by four traps.

Because most catches of *H. ensifer* were made at night in deep water, it would seem that they are not differentially entering the covered traps to seek shelter. We agree with Butler (1963) that possibly the covered traps are rendered more effective in that the bait scent is concentrated at the trap entrances, rather than diffused through the sides in addition to the entrances in the case of uncovered traps.

Five general types of bait were tested: finely ground fish, squid, shrimp (*H. ensifer*), and coarsely shopped fish and shrimp. Fish and shrimp were superior to squid and the coarsely chopped fish and shrimp outfished the finely ground containers of these species. This finely ground bait probably dispersed too rapidly. Bloody and oily fishes such as skipjack tuna (*Katsuwonus pelamis*), boarfish (*Antigonia* spp.) and *Aulopus* were found to be superior to lizardfishes (Synodontidae), flatfishes (Bothidae), and smelt (Osmeridae).

Catch rates of *H. ensifer* obtained during fall 1972 were highly variable due to the variety of traps, containers, and baits tested and the depths sampled. At this time the best catches ranged between 15 and 63 pounds (6.8 and 28.6 kg) per trap on overnight sets. One of the better catches made at this time was off the north shore of Oahu in 240 fathoms (440 m) where 122.7 pounds (55.8 kg) of *H. ensifer* were taken with four square traps baited with fish (Fig. 8). Two covered traps accounted for 108.6 pounds (49.3 kg), while two uncovered traps captured 14.4 pounds (6.5 kg).

The best single catch of *H. ensifer* was 63 pounds (28.6 kg) from a fish-baited, covered square trap during a 24-h set in 225 fathoms (410 m) north of Maui. Another covered square trap on this string, baited with shrimp, produced 24 pounds (10.9 kg), while the remaining two covered square traps also baited with fish and shrimp produced only 1.5 and 1.0 pounds (0.7 and 0.5 kg), respectively. This great disparity in the catches indicates to us that the latter two traps (which were positioned in the middle of the string) landed on end or were not fishing for some other reason.

During spring 1973, two overnight sets of six covered square traps on a string were made in 225 fathoms (410 m) off the north coast of Oahu to provide shrimp for test marketing. One string produced a total of 134 pounds (60.5 kg) of *H. ensifer*, with three traps baited with skipjack tuna accounting for 102.25 pounds (46.5 kg), and three traps baited with whitebait smelt (*Allosmerus elongatus*) taking 31.75 pounds (14.0 kg). The sec-

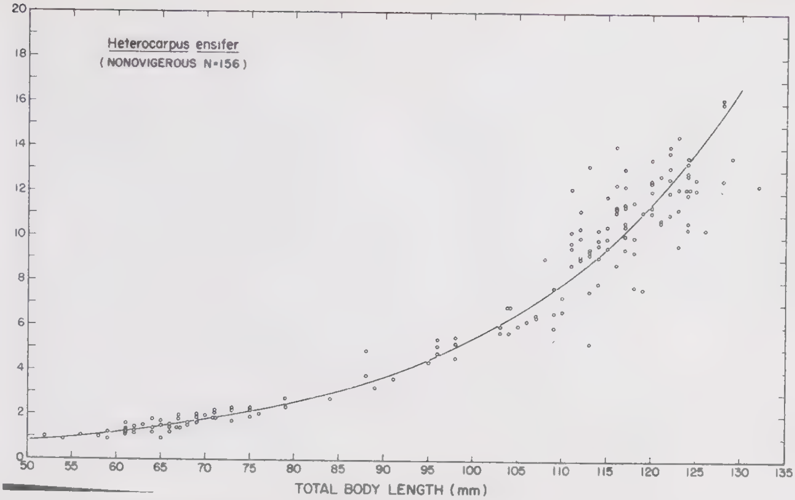


Figure 9.—Length-weight curve for 156 nonovigerous *Heterocarpus ensifer*.

ond string produced a total of 118.5 pounds (53.9 kg), the three skipjack tuna baited traps producing 80.5 pounds (36.6 kg), while the three whitebait smelt traps captured 38 pounds (17.3 kg). The tent trap was also tested on this string (baited with skipjack tuna) and produced an additional 12.5 pounds (5.7 kg). This was the single test of this trap type, and inasmuch as a square trap is about 2.1 times the volume of the tent trap, we feel that this design might eventually prove to be practical.

During August 1973, six sets of covered square traps baited with tuna were made in the 200-250 fathom (365-460 m) depth range in the Leeward Islands. The results indicated that the peak abundance of *H. ensifer* may occur deeper there than in the main group of the Hawaiian Islands. Four traps produced totals of 46.5-50 pounds (21.1-22.7 kg) at each of three sets between 225 and 250 fathoms (410 and 460 m) near Necker Island. A 6-h daytime set here in 200 fathoms (365 m) with two traps produced only 10 individual shrimp. Only 2-3 pounds (0.9-1.4 kg) of *H. ensifer* were taken in two overnight sets of four traps in 205 and 215 fathoms (375 and 390 m) near Laysan Island.

Our covered square traps were tested in a more uniform and extensive manner during May 1973 by HIMB personnel when 19 overnight sets (of 21) were made in the 200-220 fathom (365-415 m) depth range off the south coast of Oahu between Waikiki Beach and Sand Island. Four traps were fished to a string and were baited with a mixture of two species of smelt (primarily *Thaleichthys pacificus* and, to a lesser extent, *Hypomesus pretiosus*). Catches varied from 2 to 34.9 pounds (0.9 to 15.9 kg) per trap. Total catch from 70 traps (complete data not available for six traps) was about 1,015 pounds (461 kg) for an average of 14.5 pounds (6.6 kg) per trap. These data also reflect our impression that considerable variation occurs between localities and depths and even between identical trap arrangements on the same string. This is probably due to local variation in the abundance of *H. ensifer* and variation in placement of the bait container and in the trap tunnel entrances occurring during the original construction or after modification due to damage.

These catches of *H. ensifer* with covered traps generally exceeded those experienced by Clarke (1972) with uncovered traps outside Kaneohe Bay on the northeast coast of Oahu during November 1970. Catches there for nine quantitative sets in the 150- to 250-fathom depth range varied from 0.6 to 11.9 pounds (0.3 to 5.4 kg) per trap and averaged 4.5 pounds (2.0 kg). At that time the best catch obtained was a respectable 96 pounds (43.6 kg) from eight traps fished in 200 fathoms (365 m).

We have taken *H. ensifer* in depths ranging from 76 to 360 fathoms (137 to 660 m). Clarke (1972) took the species between 80 and 400 fathoms (146 and 730 m) but concluded that it is most abundant between 150 and 250 fathoms (275 and 455 m). Our results indicate a peak abundance between 200 and 240 fathoms (365 and 440 m), but we have few stations in depths between 150 and 200 fathoms (275 and 365 m). Quite probably the depths of peak abundance for *H. ensifer* vary locally according to variations in the temperature structure. In the main group of the Hawaiian Islands, bottom temperatures are about 14°C at 150 fathoms (275 m), 9.5°C at 200 fathoms (365 m), and 8°C at 250 fathoms (455 m).[3]

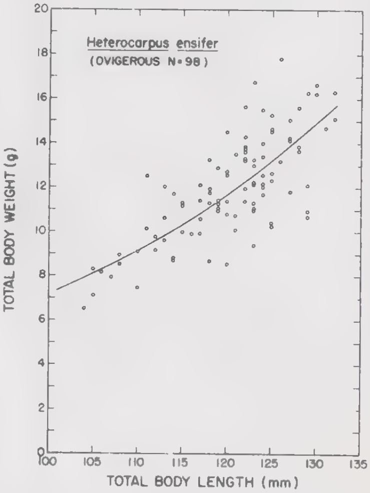


Figure 10.—Length-weight curve for 98 ovigerous *Heterocarpus ensifer*.

Clarke (1972) also demonstrated that the 150- to 250-fathom depth range was the zone where the largest size-class of shrimp occurred. The catches in greater and lesser depths were comprised of a significantly greater portion of smaller individuals. We did not collect extensive length-frequency information, but estimations of the size composition of the catches also indicate that smaller shrimp are found above and below the depths of peak abundance.

Clarke (1972) pointed out that *H. ensifer* seems to exhibit protandrous hermaphroditism (sex change from male to female with growth), but that the situation seems to be more complex than for some of the commercial pandalid shrimps in that a large portion of the males reach near-maximum size without transforming and that many small individuals (below egg-bearing size) are females. A large proportion of the larger females taken are ovigerous (gravid, or "berried") throughout the year. Clarke (1972) presented data that indicated that this condition varied with depth and that the proportions may vary seasonally.

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[3] Unpublished data, Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, HI 96812.

The largest size-group of *H. ensifer* taken in our traps usually weighed about 35 to 45 individuals per pound (75 to 100/kg) with the heads on, although the largest individuals taken run 28-30 per pound (62-66/kg). We obtained total length (tip of rostrum to tip of teison) and weight data for 156 nonovigerous *H. ensifer* (Fig. 9) and 98 ovigerous females (Fig. 10). Data were obtained from specimens frozen less than a month, thawed, and damp-dried. The fitted exponential length-weight curve for the nonovigerous individuals is: $\log_{10} W = 0.0162\,L - 0.8789$, where W = total weight in grams, and L = total length in millimeters; $r^2 = 0.972$. The equation for the ovigerous individuals is: $\log_{10} W = 0.0105\,L - 0.1947$, where $r^2 = 0.589$, W = total weight in grams, and L = total length in millimeters.

We also determined the percentage of the total weight contributed by the tails of ovigerous and nonovigerous individuals, both with and without shell and eggs (Fig. 11). The majority of ovigerous individuals have total tail weights making up about 45-55 percent of the total weight, whereas the tail weights of most of the nonovigerous individuals were about 40-50 percent of the total weight (Fig. 11A and B). These data indicate that the egg mass is about 5-10 percent of the total body weight. With the shell and eggs removed, the tail muscle of both ovigerous and nonovigerous individuals make up about 25-35 percent of the total weight (Fig. 11C and D).

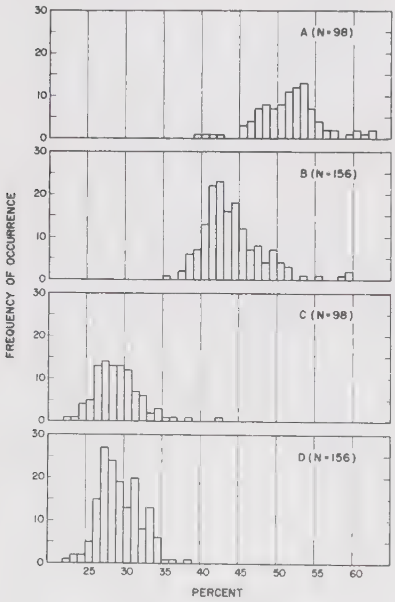

Figure 11.—*Heterocarpus ensifer.* Weight of tail with shell as percent of total weight: A. Ovigerous females; B. Nonovigerous individuals. Weight of tail without shell as percent of total weight: C. Ovigerous females; D. Nonovigerous individuals.

Trapping for *Heterocarpus laevigatus*

H. laegivatus (Fig. 1) is a large species of *Heterocarpus* inhabiting a deeper depth range than *H. ensifer*. Clarke (1972) collected this species between 200 and 400 fathoms (365 and 730 m), while we have obtained it in depths ranging from 235 to 450 fathoms (430 to 825 m). We have rather limited coverage in the deeper portion of this depth range, but several catches indicate that this species can be taken in sufficient quantities to support a commercial fishery. Our initial catches with uncovered traps were not encouraging, and were similar to those experienced by Clarke (1972) where yields were usually on the order of 1.5 pounds or less per trap.

Some of the better catches of *H. laevigatus* we obtained with covered traps are as follows. South coast of Oahu: 18 pounds (8.2 kg), three traps, 246 fathoms (450 m); 10.6 pounds (4.8 kg), two traps, 255 fathoms (465 m). North coast of Oahu: 11.1 pounds (5.0 kg), two traps during a 4-h daytime set, 285 fathoms (520 m). Kawaihae, Hawaii: 7 pounds (3.2 kg), two traps, 238 fathoms (435 m). Leeward Islands: 15 pounds (6.8 kg), four traps, 320 fathoms (585 m), Pioneer Bank; 34.8 pounds (15.7 kg), four traps, 360 fathoms (660 m), French Frigate Shoal; 7 pounds (3.2 kg), four traps, 440 fathoms (805 m), Pioneer Bank. Although the data are rather fragmentary, it would appear that this species is most abundant in depths of about 240 to 375 fathoms (440 to 684 m).

The proportion of large and small individuals of *H. laevigatus* taken in the traps also seems to vary between catches, but the pattern is not yet clear. Large individuals of this species attain lengths of 200-220 mm total length, but most of the individuals comprising the largest size-group range from 150 to 175 mm total length and average 8-11 individuals per pound (heads on).

FURTHER CONSIDERATIONS

One problem encountered with *H. ensifer* is cannibalism of a certain percentage of the trapped individuals. We have no precise data on this phenomenon, but rough estimates indicate that as little as 1 percent to as much as 15 percent of all the individuals in a trap may be affected. Subjectively, it seemed that the highest rates of cannibalism occurred in sets of long duration or in traps in which the bait supply was exhausted. Larger individuals are most often affected, and, if ovigerous, the eggs and swimmerets are removed first. Then the viscera, and, finally, the tail musculature are attacked. This results in the problem of sorting the husks and partially devoured individuals which contaminate the catch. Culling of cannibalized and small shrimp was most easily effected in a bath of seawater.

We point out that the traps used in these preliminary trials evolved during usage, and certainly do not represent what may become the optimum design and construction. Probably any container utilizing the principle of the covered trap with a long tapered tunnel would be suitable. The mesh size of the tunnels should be increased to about 0.75 inch (19 mm) to permit escapement of small shrimp. Possibly a trap with an entrance on one end and a flat screen on the other end would permit escapement of small individuals during hauling of the trap, thus reducing the amount of sorting on the fishermen's part and preventing the premature harvest of young shrimp.

The tail meat of the two species of *Heterocarpus* tends to break down rapidly when the shrimp are improperly chilled aboard the vessel. The shrimp must be immediately placed in crushed ice or chilled seawater. This will provide an acceptable product for up to about 3 days after capture. We found that cooking the shrimp right after capture resulted in chilled shelf life of 3 to 4 days. One test of immediate freezing of raw shrimp in a brine solution at about −20°C resulted in an acceptable product. After freezing, the shrimp were placed in a conventional freezer and tested at intervals over a 2-week period. Very little salt was taken up by the shrimp and the product did not seem to deteriorate during the brief test period.

Care must be taken not to overcook these species. Boiling times of 2-4 min are adequate for the frozen *H. ensifer*. The tail meat can be shelled easily for other methods of preparation by briefly thawing in running water or after a 30-sec blanch.

The only present commercial fishery for a species of *Heterocarpus* (*H. reedi* Bahamonde) exists primarily off Chile, and to a lesser extent, Peru. In this highly productive region of upwelling, a trawl fishery produces about 10,000 metric tons annually (Hancock and Henriquez, 1968). It has been estimated that the total available grounds are about 1,600 km² in extent and that production could reach about 20,000 metric tons annually (Gulland, 1971). This indicates an annual production of about 12.5 metric tons/km².

In Hawaii, it appears that the abundance of *H. ensifer* is greatly underestimated by sampling with 41-foot shrimp trawls. Our maximum catch rate for this species was 240 kg/km² although most catches were less than 10 percent of this. It is perhaps best at present to not speculate on the area effectively fished by a single shrimp trap, but rather point out again that traps are a much more efficient means of harvesting *H. ensifer* in Hawaii. We feel that an annual yield of 1 or 2 metric tons/km² for Hawaiian waters does not seem like an unreasonable estimate. The total area of the optimum depth range for *H. ensifer* in the main group of the Hawaiian Islands has not been precisely determined, but probably exceeds 1,000 km².

It would seem that *H. ensifer*, an almost entirely cosmopolitan species occurring from Hawaii to the western central Atlantic, is about as abundant in other parts of its range as in Hawaii. In the western Atlantic, exploratory trawl catches by the NMFS were of the same magnitude as were those in Hawaiian waters.[4] Limited trapping near Guam in the western Pacific[5] have produced catches similar to those reported here.

Using data presented by Moiseev (1969), it was calculated that the 200- to 1,000-m depth zone of the world continental and insular slopes in regions where species of *Heterocarpus* may occur has a total area of about 5 million km². We assume that the area of the 200-600 m depth range is about half this: 2.5 million km². Assuming that 10 percent of this area is fishable and supports concentrations of shrimp, we have a potential fishing area of approximately 250,000 km². If yields on the order of 1-10 metric tons/km² are realistic, then it seems probable that *H. ensifer* and other members of this genus represent an unexploited resource of considerable magnitude.

ACKNOWLEDGMENTS

We thank William Van Heukelem for providing catch data obtained with the FV *Valiant Maid* and Bernard Ito for the photographs of the traps. Thomas A. Clarke and Lael L. Ronholt made pertinent comments on the manuscript. Richard B. Roe provided exploratory trawling data for the western central Atlantic. The illustrations are by Tamotsu Nakata.

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MFR Paper 1095. From Marine Fisheries Review, *Vol. 36, No. 10, October 1974. Copies of this paper, in limited numbers, are available from D83, Technical Information Division, Environmental Science Information Center, NOAA, Washington, DC 20235.*

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[4] Data from Pascagoula Fishery Products Technology Laboratory, Pascagoula, MS 39567.

[5] L. G. Eldridge, University of Guam, Agana, Guam 96910. Pers. comm.

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BOTHUS THOMPSONI (FOWLER) 1923, A VALID SPECIES OF FLATFISH (PISCES:BOTHIDAE) FROM THE HAWAIIAN ISLANDS

Paul Struhsaker and Robert M. Moncrief[1]

ABSTRACT

Bothus thompsoni (Fowler) 1923 is resurrected from the synonymy of *B. bleekeri* Steindachner and redescribed. *B. thompsoni* differs from all other recognized species of the genus in possessing 11-17 gill rakers on the lower limb of the first gill arch and 115-147 lateral line scales. *B. thompsoni* is endemic to the Hawaiian Islands where it inhabits the outer shelf in depths of 70-115 m.

Fowler (1923) proposed *Platophrys thompsoni* on the basis of a single specimen obtained by John W. Thompson. Although no exact locality data were given, we assume the specimen was from the Honolulu market. *Platophrys* is now considered a synonym of *Bothus*, while Norman (1934), without comment, relegated *Bothus thompsoni* to the synonymy of *B. bleekeri* Steindachner. Gosline and Brock (1960) followed Norman in listing *B. bleekeri* from the Hawaiian Islands. Previously, only the holotype of *B. thompsoni* was available for study. Our examination of numerous specimens collected by the National Marine Fisheries Service (NMFS) during recent bottom trawling surveys in the 60-700 m depth range of the Hawaiian Islands demonstrates that *B. thompsoni* should be recognized as a valid species.

MATERIAL AND METHODS

All specimens were collected with 12.5-m (headrope) shrimp trawls during bottom trawling surveys in the Hawaiian Islands with the NMFS RV *Townsend Cromwell.* Sampling effort and general ichthyological results of these surveys are given by Struhsaker (1973). Most specimens examined (one exception from Maui) were from the north coast of the island of Oahu.

The following description is based on a series of 29 male (55.8-114.4 mm SL) and 31 female (39.1-103.7 mm SL) specimens all of which are housed in the National Museum of Natural History (USNM) and Bernice P. Bishop Museum (BPBM). Additionally, 33 uncatalogued specimens cleared and stained by the method described by Taylor (1967) were utilized in vertebral and gill raker counts, and more uncatalogued specimens were examined, obtaining supplementary dorsal, anal, and caudal ray counts.

Measurements and counts are usually as defined by Norman (1934), Hubbs and Lagler (1958), and Gutherz (1967). Standard length was taken from tip of snout to end of hypural plate on the blind side. Horizontal eye diameter was taken between edges of the bony orbits. Snout to axis of greatest depth was taken from the snout to a vertical line at the greatest body depth. The last two dorsal and anal rays are each associated with pterygiophores and are counted as two. Lateral line scale rows just above the lateral line and pored lateral line scales were counted. Vertebral counts were taken from radiographs and from cleared and stained specimens. Gill rakers were counted as discussed below.

To evaluate morphometric characters, measurements in original units and as percent of standard length were plotted as functions of standard lengths.

RESULTS

Description

Although a figure of *B. thompsoni* did not accompany the original description, Fowler (1928), in listing the species for Oceania, provided a figure of the type (P1. IV, C) which is

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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housed in the BPBM (3398). Measurements of the 106.8 mm SL male holotype (Fowler gave an undefined length of 134 mm) expressed as percent of standard length are given in Table 1. We obtained the following counts on this specimen: dorsal rays 86; anal rays 62; caudal rays 16; pectoral rays (both sides) 12; lateral-line scale rows 130; pored lateral-line scales 83; gill rakers 19 (5 + 14). Fowler (1923) gave counts of 132 scale rows and 20 gill rakers (6 + 14). Otherwise, our counts agree with his.

Photographs of recently collected female (106.4 mm SL) and male (114.4 mm SL) specimens (both BPBM 14102) are shown in Figures 1 and 2.

Counts

Dorsal and anal ray counts, expressed as bivariate relations, for 101 specimens are given in Table 2. Dorsal rays ranged from 84 to 95 ($\overline{X} = 87.9$) and anal rays ranged from 64 to 70 ($\overline{X} = 66.3$). Although the dorsal ray counts are skewed to the right, the distribution does not deviate significantly from a normal distribution ($P > 0.2$; Kolomogorov-Smirnov test for goodness of fit, $D = 0.0702$).

There were considerably fewer pored lateral-line scales (Table 3) ($\overline{X} = 80.9$) than the number of vertical scale rows above the lateral line ($\overline{X} = 131.6$).

There was a tendency towards more pectoral rays (Table 3) on the ocular side ($\overline{X} = 12.24$) than on the blind side ($\overline{X} = 11.49$). The upper pectoral ray on the ocular side is reduced and sometimes inconspicuous. The upper pectoral ray on the blind side is also reduced, but easily visible.

Bothus thompsoni appears to be unique among species of *Bothus* in usually possessing 16 caudal rays. Of 163 specimens examined (Table 3), 2 (1.2%) had 15 rays, 157 (96.3%) had 16 rays, and 4 (2.5%) had 17 rays. The caudal rays are usually associated with the four hypural elements. Of 31 cleared and stained specimens having 16 rays, 11 had a caudal ray formula of 4-4-4-4 (dorsal element counted first). Other formulae obtained and number of specimens are as follows (rays articulating between elements are enclosed by parentheses): 4-4-3-(1)-4, (6 specimens); 4-4-3-5, (5 specimens); 3-(1)-4-4-4, (4 specimens); 3-(1)-4-3-(1)-4, (2 specimens); 3-(1)-4-3-5, (1 specimen); 3-(1)-4-3-5, (1 specimen); 4-4-3-5, (1 specimen). Two specimens with 15 rays had formulae of 4-4-3-4 and 3-(1)-4-4-3.

None of the caudal rays of *B. thompsoni* was associated with the neural and haemal spines of the penultimate vertebra or articulated in the space between the spines and hypural elements. Thus, *B. thompsoni* differs from certain other species of *Bothus* which have rays associated with the neural and haemal spines of the penultimate vertebra or which occur in the interspace between the spines and hypural elements. Gutherz (1970) gives a formula of 1-4-4-3-4-1 for larval *Bothus* (species not determined) from the western North Atlantic. We obtained the same formula for 12 cleared and stained specimens of *B. pantherinus* (Rüppell) from the Hawaiian Islands. In these specimens the first and last rays most often articulated in the interspace between the spines and hypural elements. These

TABLE 1.—*Bothus thompsoni:* Measurements of 13 characters for holotype, 29 males, and 31 females expressed as percent of standard length. Holotype excluded from regression statistics (a = ordinate intercept, b = regression coefficient).

Characters measured	Holotype BPBM 3398 percent of standard length	Range percent standard length for males	a	b	r^2	Range percent standard length for females	a	b	r^2
Head length	28.5	25.7-29.5	0.646	0.270	0.965	26.0-29.6	1.100	0.264	0.983
Snout length: to upper eye	23.9	14.0-21.5	−5.865	0.252	0.961	13.0-16.6	−1.022	0.162	0.968
to lower eye	6.3	4.4- 6.2	0.315	0.048	0.821	4.8- 6.8	−0.171	0.569	0.857
Orbit diameter: upper	11.6	9.1-12.6	2.255	0.084	0.828	8.2-12.4	1.656	0.087	0.896
lower	9.6	7.6-10.9	2.222	0.071	0.811	8.0-11.5	2.263	0.067	0.874
Interorbital distance	14.9	7.7-13.5	−5.856	0.182	0.958	5.1- 8.6	−1.112	0.088	0.949
Length of upper jaw	10.3	8.0-10.6	1.102	0.081	0.856	8.2-10.4	0.770	0.084	0.943
Greatest body depth	60.8	57.7-66.0	−1.046	0.629	0.968	57.0-67.3	−0.057	0.632	0.973
Least depth caudal peduncle	11.2	9.7-11.4	0.042	0.107	0.970	9.2-11.6	0.195	0.104	0.981
Length of pectoral fin: ocular side	21.7	19.0-24.7	4.661	0.159	0.912	18.8-24.9	4.925	0.153	0.924
blind side	18.4	15.3-18.7	2.294	0.141	0.928	14.0-18.5	0.826	0.155	0.930
Length of anal fin base	75.2	73.4-77.4	2.373	0.734	0.958	71.9-84.8	−3.634	0.814	0.966
Snout to greatest body depth	46.3	41.6-48.6	−4.156	0.497	0.959	41.4-50.0	0.341	0.452	0.961

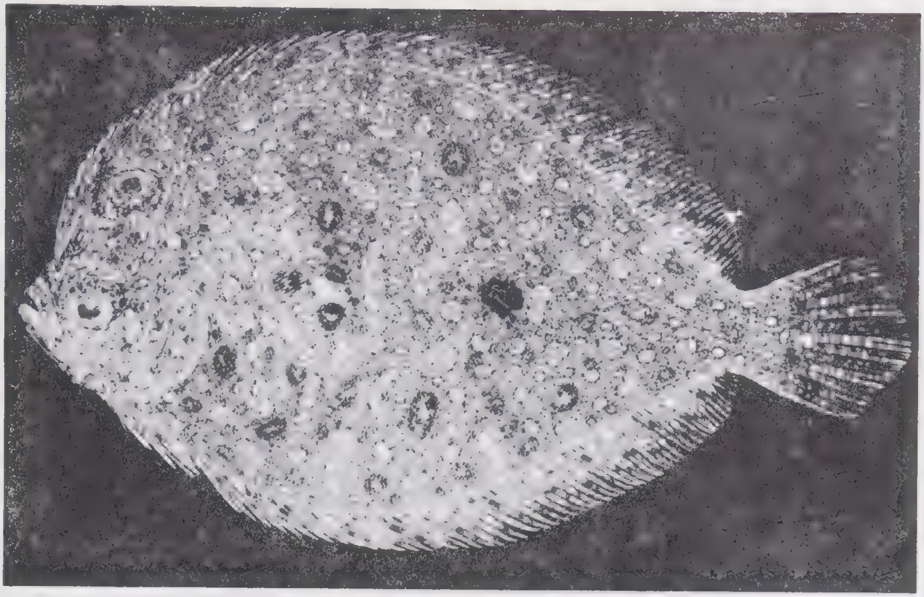

FIGURE 1.—A 106.4 mm SL female *Bothus thompsoni*.

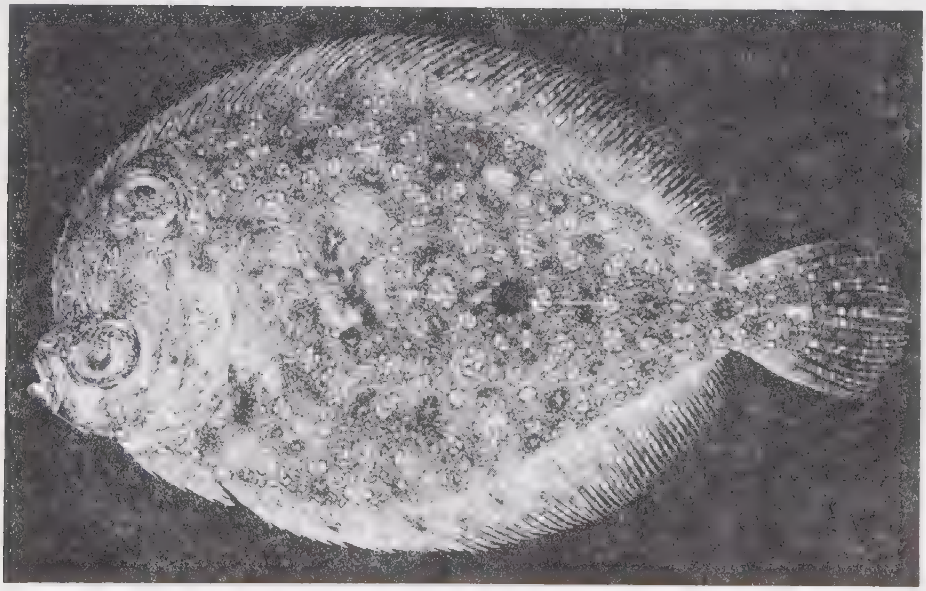

FIGURE 2.—A 114.4 mm SL male *Bothus thompsoni*.

data indicate that *B. thompsoni* exhibits a more variable caudal ray formula than *B. pantherinus*.

The first two and last two caudal rays of *B. thompsoni* are usually simple. Of a sample of 20 specimens, only 2 (10%) had either the second or penultimate ray divided.

The arrangement of gill rakers in *B. thompsoni* is shown in Figure 3, and counts are given in Table 3. There are 3-9 reduced gill rakers associated with the epibranchial and 1-4 reduced gill rakers associated with the hypobranchial. A series of 9-14 well-developed gill rakers is principally associated with the ceratobranchial. The reduced gill rakers associated with the epibranchial comprise the counts for the upper limb of the gill arch. The first well-developed

TABLE 2.—Dorsal and anal ray counts for 101 specimens of *Bothus thompsoni*.

Number of anal rays	Number of dorsal rays 84	85	86	87	88	89	90	91	92	93	94	95	Total number of specimens
70	—	—	—	—	—	—	1	—	—	—	—	1	2
69	—	—	—	—	—	1	—	1	—	—	—	—	2
68	—	—	—	—	1	3	1	4	1	—	—	—	10
67	—	—	2	5	7	7	5	3	1	—	—	—	30
66	—	3	7	3	9	8	—	—	—	—	—	—	30
65	2	—	8	7	3	—	—	—	—	—	—	—	20
64	2	1	2	1	1	—	—	—	—	—	—	—	7
Total number of specimens	4	4	19	16	21	19	7	8	2	—	—	1	101

raker occurs at the angle of the arch and is included in the counts for the lower limb, although stained material reveals this raker to be more closely associated with the epibranchial. The last one or two well-developed rakers are associated with the hypobranchial.

The number of gill rakers in the size range examined is apparently independent of size. A regression coefficient calculated for 28 females was not significant ($P > 0.4$).

Vertebral counts were obtained from 96 specimens. There are usually 10 abdominal vertebra (94 specimens), but two individuals had 11 (28 caudal vertebrae in both cases). Counts of caudal vertebrae (including urostyle) were 27 (7), 28 (69), and 29 (18), while total vertebral counts were 37 (7), 38 (69), and 39 (20).

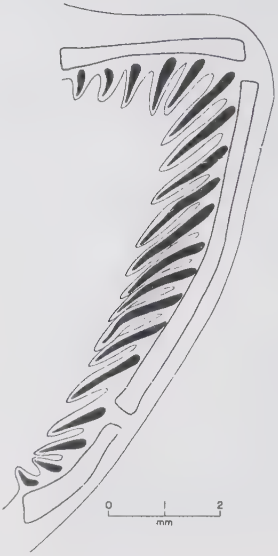

FIGURE 3.—A typical first gill arch from the ocular side of *Bothus thompsoni*.

Measurements

The measurements obtained from 29 male and 31 female specimens for 13 characters are summarized in Table 1. Linear regressions were calculated in original units of measurement (mm) with standard length as the independent

TABLE 3.—*Bothus thompsoni:* Counts for eight characters.

Characters	Frequency of occurrence 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	*N*	$\overline{X}$
Caudal rays	-	-	-	-	-	-	-	-	-	-	-	-	2	157	4	-	-	-	-	-	-	-	163	16.01
Pectoral rays (ocular side)	-	-	-	-	-	-	-	1	7	32	22	1	-	-	-	-	-	-	-	-	-	-	63	12.24
Pectoral rays (blind side)	-	-	-	-	-	-	-	2	29	31	1	-	-	-	-	-	-	-	-	-	-	-	63	11.49
Gill rakers (upper limb)	1	5	29	29	21	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	91	5.92
Gill rakers (lower limb)	-	-	-	-	-	-	-	-	1	3	21	22	27	13	4	-	-	-	-	-	-	-	91	14.38
Gill rakers (total)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	11	13	24	9	17	6	5	91	20.30
	70-71	72-73	74-75	76	78	80	82	84	86	88	90-91	92-93												
Pored lateral line scales	1	-	-	5	6	8	3	4	2	1	-	1											31	80.9
	114-115	116-117	118-119	120-121	122-123	124	126	128	130	132	134	136	138	140	142	144	146-147							
Lateral line scale rows	1	-	-	-	4	2	6	6	17	5	6	8	5	-	1	-	2						63	131.6

variable. Plots of all regressions are linear and exhibit high r^2 values.

The regressions obtained for the 13 measured characters were subjected to analysis of covariance to test for sexual dimorphism. Highly significant differences ($P<0.001$) were found between the regression coefficients for two characters (which are related): interorbital distance (Figure 4) and snout to upper eye. Juvenile and adult male specimens of *B. thompsoni* are similar to many *Bothus* spp. males in possessing a much greater interorbital distance than females of the same species. Male *B. thompsoni* exhibit positive allometric growth of the interorbital distance, this measurement being about 7.5%-9.0% of standard length at a length of 50-60 mm and about 12%-14% of standard length at a length of 100-115 mm. In female specimens longer than 50 mm the interorbital distances were 6.0%-8.6% of standard length. Interorbital distances of 5.3% and 5.1% of standard length were noted in two specimens 39 mm and 48 mm long. As expected, male *B. thompsoni* exhibited positive allometric growth of the snout to upper eye distance.

Among the remaining 11 characters subjected to analysis of covariance, there were no significant differences between regression coefficients. There were significant differences ($P<0.05$) in the elevations of the regressions between sexes for four characters. Both the upper and lower orbit diameters of males tend to be larger than for females; the differences in adjusted means for the two characters are 0.35 and 0.40 mm, respectively. Females tend to have a greater body depth and a greater snout to greatest body depth distance. The differences in adjusted means for these two characters are 1.1 and 1.0 mm, respectively.

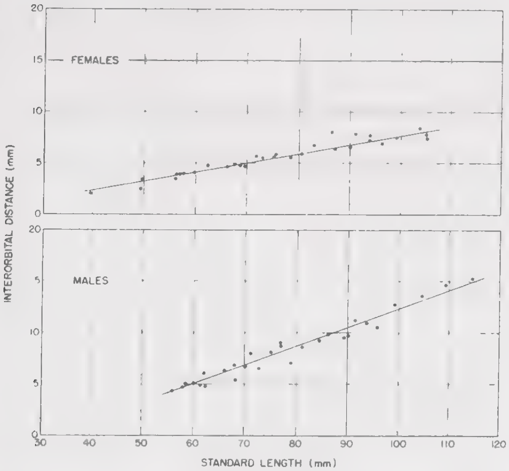

FIGURE 4.—Plots of the interorbital distance of 29 male and 31 female specimens of *Bothus thompsoni*.

In both sexes, the pectoral fins of the ocular side tend to be longer than those of the blind side (Table 1). The pectoral fins of both sexes exhibit negative allometric growth. This is most pronounced on the ocular size where the pectoral length is about 24%-25% of standard length at 40-60 mm and about 18%-21% of standard length at a length of 100-115 mm. There is only slight negative allometric growth of the pectoral fin on the blind side where this structure varies from 14.0% to 18.7% of standard length.

All other morphometric characters examined exhibited approximately isometric growth.

Two of the measurements we obtained for the holotype (Table 1) do not fall within the ranges we obtained from our study series: interorbital distance and snout to upper eye.

Other morphological characters

Bothus thompsoni has cycloid scales on the blind side and on most of the ocular side (Figure 5A). Ctenoid scales occur on the proximal portions of the dorsal and anal rays. There are 2-3 rows of ctenoid scales at the bases of the dorsal and anal fins (Figure 5B). Fowler (1923) stated that the holotype had ctenoid scales on the cheeks and postorbital region. In addition, we find that there is a patch of about 15 ctenoid scales below the curved portion of the lateral line in the holotype. A scale from this region is shown in Figure 5C. The occurrence of ctenoid scales on the cheek and in the vicinity of the curved portion of the lateral line is a variable character. Of 25 specimens (67.5-106.4 mm SL) from our study series, six had ctenoid cheek scales, three had ctenoid scales on the cheek and near the lateral line, and one had ctenoid scales near the lateral line only. The presence of ctenoid scales in these two regions does not appear to be related to size or sex. The cycloid scales are small and nonimbricated, but the ctenoid scales at the dorsal and anal fin bases overlap to a slight degree. The ctenii of the ctenoid scales generally occur in two rows: a primary row of well-developed ctenii and a secondary row of smaller ctenii basal to the

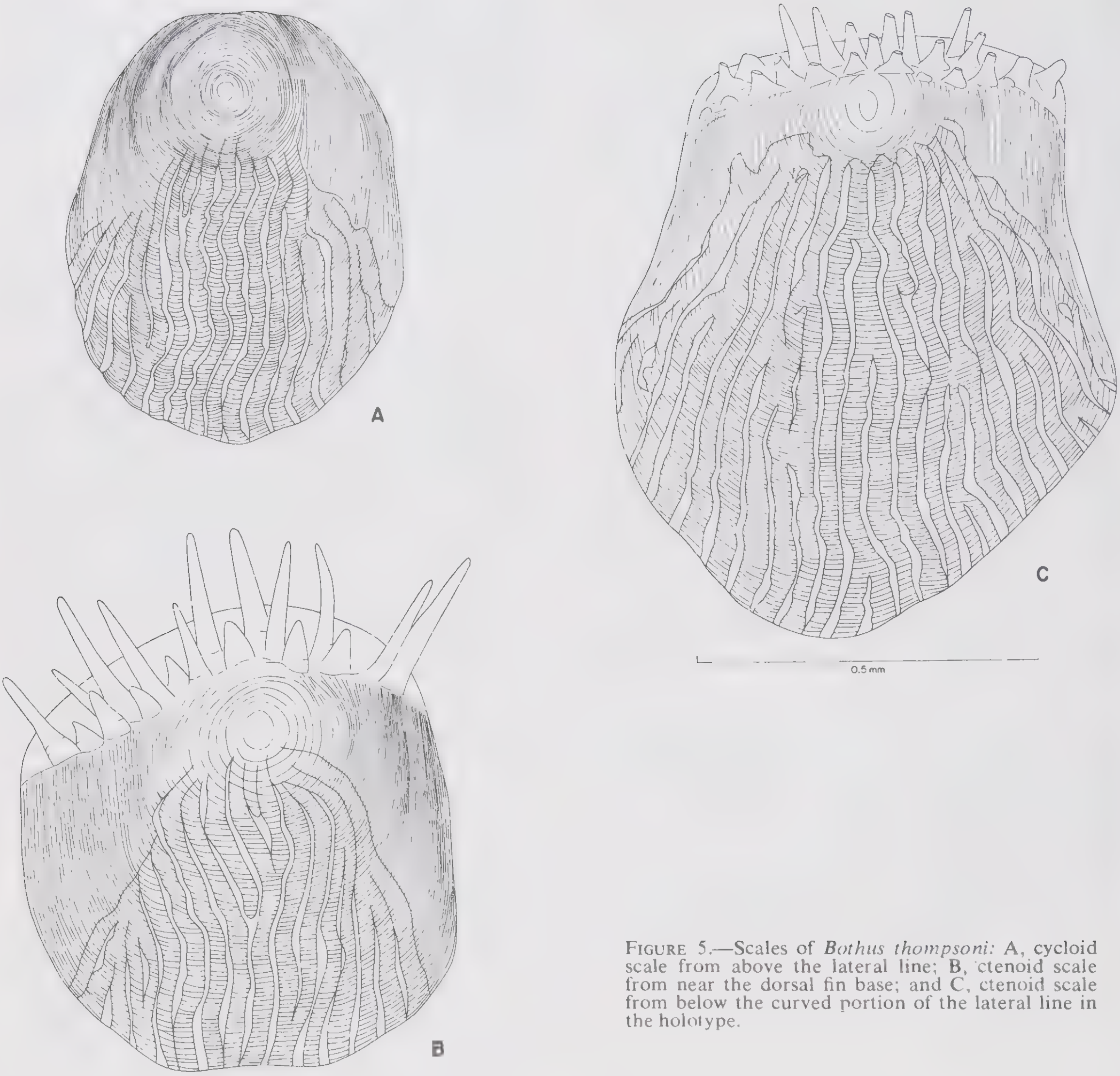

FIGURE 5.—Scales of *Bothus thompsoni:* A, cycloid scale from above the lateral line; B, ctenoid scale from near the dorsal fin base; and C, ctenoid scale from below the curved portion of the lateral line in the holotype.

primary row (Figure 5B and C). The number of ctenii on cheek scales varies from 5 to 8, while scales from the dorsal and anal fin bases at the greatest body depth have 15 to 25 ctenii.

The general arrangement of teeth in the upper and lower jaws is shown in Figure 6. There are usually three rows of teeth. The outer row consists of a few, stout conical teeth in the anterior portion of the jaws. The middle row consists of more numerous, but less stout, conical teeth. The inner row consists of depressed, poorly ossified conical teeth subequal in number to those in the middle row (except on the blind side of the upper jaw). The inner row of teeth are movable, being held in place by flesh and not inserted in the jaw bones.

The number of outer teeth, and, to a lesser extent, the middle teeth, vary according to jaw bone and size of specimen. This is illustrated in Figure 7 where the number of teeth are plotted by standard length for 10 females 49.2-106.4 mm SL and 10 males 55.8-114.5 mm SL. The increase in number of outer teeth with size is apparent for all jaw bones except the dentary on the ocular side. There also appear to be more outer teeth in the premaxillary of the ocular side of the males.

The teeth in the middle row also exhibit a general, but less well-defined, increase in numbers with size.

There are no fleshy papillae along the edges of the eyes such as reported for male *B. pantherinus* (Norman, 1934). There is a single prominent, blunt protuberance on the snout of males greater than 60 mm SL. This structure is represented in females by a small knob. The anterior edge of the lower orbit tends to be more developed and rugose in males than in females.

Coloration of fresh specimens

The blind side of both sexes is white, but tending to dusky white in males greater than about 80 mm SL, especially on the cheek and above the cheek. The ground color of the ocular side is light olive green. There is a single prominent dark spot on the lateral line posteriad about 60% of the standard length. There are two secondary dark ocelli near the pectoral fin. There are 14-15 olive green ocelli broadly distributed along the dorsal and ventral borders of the trunk. There are numerous light blue ocelli and spots distributed over the trunk, head, and dorsal, anal, caudal, and ventral fins. The pectoral fins are almost clear. In males, the light blue spots are more numerous and elongated along the anterior profile and between the eyes.

Comparison with Other Species of *Bothus*

A definitive discussion of the relation of *B. thompsoni* to other species of *Bothus* must await further study of the genus on a worldwide basis. *B. thompsoni* differs from all recognized species of *Bothus* (Fowler, 1933; Norman, 1934; Chabanaud, 1942; Stauch, 1966; Gutherz, 1967; Amaoka, 1969; Topp and Hoff, 1972) in possessing 11-17 gill rakers on the lower limb of the first arch (11 or fewer in other species) and 115-147 scale rows above the lateral line (apparently 100 or fewer in other species: Norman, 1934). It may also be unique in that it usually has only 16 caudal rays as opposed to 17 in other species. This character, however, apparently has been examined only rarely by earlier authors and few data on the numbers and arrangements of the caudal rays are available (Chabanaud, 1942; Amaoka, 1969; Gutherz, 1970). The figures given by Norman (1934) for *B. leopardinus* (Günther) and *B. bleekeri* indicate caudal ray counts of 16. However, a count of 16 is also indicated for *B. ovalis* (Regan) which Amaoka (1964) has shown to be the young of *B. myriaster* (Temminck and Schlegel). *B. myriaster* has 17 caudal rays (Amaoka, 1969). Chabanaud (1942) described *B. budkeri* from the Red Sea and gave caudal ray counts of 16 for the holotype and 17 for the two paratypes. A sample of 368 adult and larval specimens of *B. pantherinus* from the Hawaiian Islands had the following caudal ray counts: 16 (2.7%), 17 (95.7%), 18 (1.6%). Further examination of this character is required.

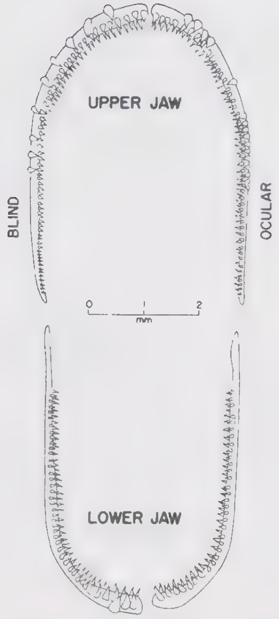

FIGURE 6.—The arrangement of teeth in *Bothus thompsoni*.

We have not examined specimens of *B. bleekeri*, and we separate this species from *B. thompsoni* on the basis of the description given by Norman (1934). In addition to the differences in gill raker and lateral line scale row counts discussed above, *B. thompsoni* has more pectoral rays on the ocular side (10-14 vs. 8-9). Adult male specimens of *B. thompsoni* do not have elongated pectoral rays (ocular side), whereas male *B. bleekeri* have elongated pectoral rays.

Two other species of *Bothus*, *B. pantherinus* and *B. mancus* (Broussonet), occur in the Hawaiian Islands. Adult specimens of *B. thompsoni* may be separated from similar life history stages of the former two species on the basis of body profile alone. Other useful characters for distinguishing *B. thompsoni* from *B. pantherinus* and *B. mancus* (in addition to counts of the lateral line scale rows, lower gill rakers, and caudal rays) are as follows. Cycloid scales are present on the ocular side of *B. thompsoni* (except at the bases of the dorsal and anal fin, and occasionally on the cheeks and in the vicinity of the lateral line) as opposed to ctenoid scales on the ocular side for *B. pantherinus* and *B. mancus.* Adult males of the latter two species have elongated pectoral fin rays on the ocular side, while male specimens of *B. thompsoni* do not. *Bothus mancus* possess more dorsal and anal fin rays than do *B. thompsoni* and *B. pantherinus* (97-102 vs. 84-96 and 77-82 vs. 64-74, respectively; Hawaiian Island

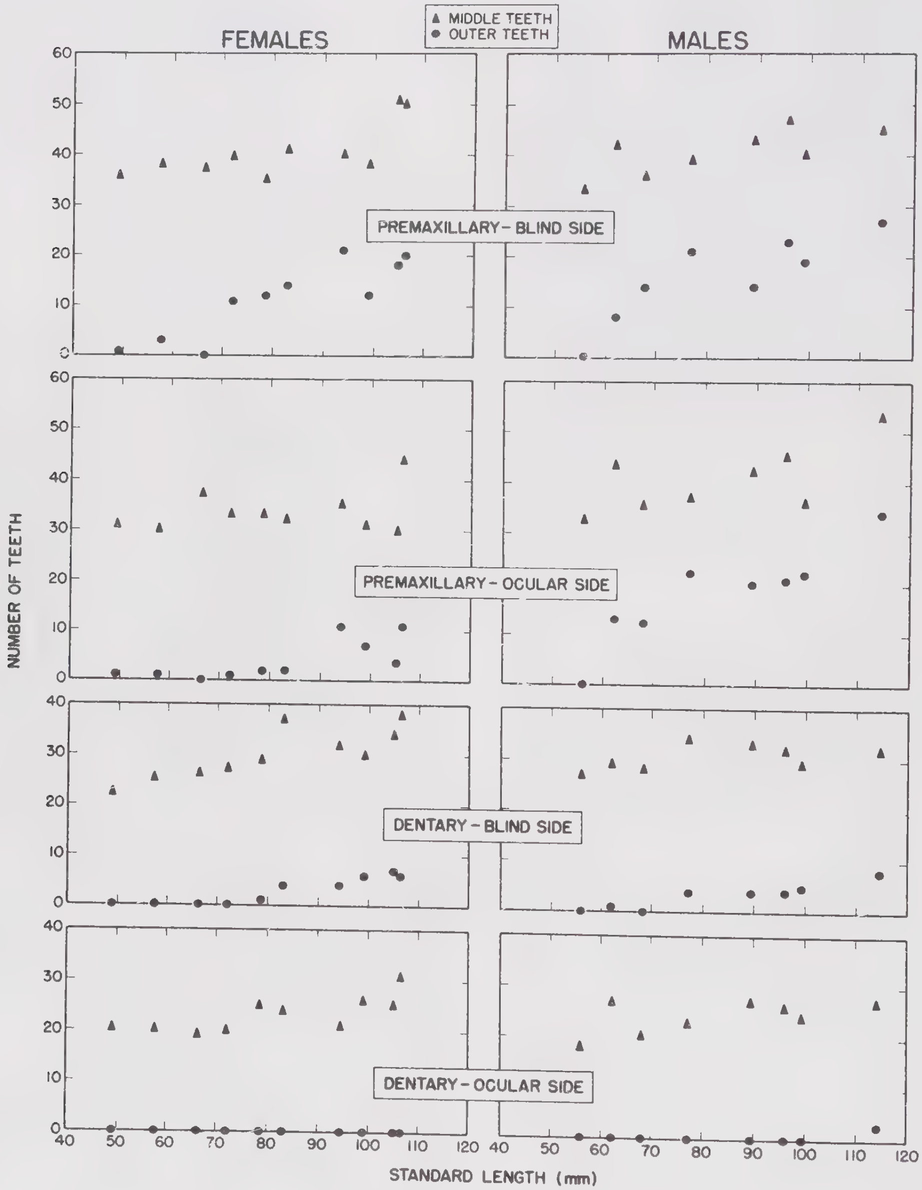

FIGURE 7.—Numbers of teeth in the outer and middle tooth rows in *Bothus thompsoni.*

specimens). *Bothus thompsoni* has 10-14 pectoral rays, whereas this count is 9-11 for both *B. pantherinus* and *B. mancus.*

With regard to other Indo-Pacific species recognized by Norman (1934), *B. thompsoni* differs from *B. myriaster* in that the pectoral fins of males are not elongated in the former species. The combination of cycloid and ctenoid scales on the ocular side of *B. thompsoni* differentiates it from *B. assimilis* (Günther) which has only cycloid scales and from *B. leopardinus* (Günther) which has only ctenoid scales on the ocular side (Norman, 1934). Norman (1934) considers also that *B. constellatus* (Jordan, *in* Jordan and Goss) is very doubtfully distinct from *B. leopardinus.*

Although no illustration was given of *B. budkeri* (Chabanaud, 1942) from the Red Sea, it differs from *B. thompsoni* in having a lesser body depth, fewer dorsal and anal rays, fewer gill rakers on the lower limb of the first arch, and only ctenoid scales on the ocular side.

Fowler (1933) described five species of *Bothus* from the Philippines and China Sea. The generic placement of several of these species is questionable. At any rate, none of them could be confused with *B. thompsoni.*

Ecology

With the exception of one specimen caught at a depth of 72 m off Maui, all specimens of *B. thompsoni* taken to date have come from depths of 90-113 m off the north coast of Oahu where bottom temperatures ranged from 24.5° to 26.0°C. About 580 specimens (32-107 mm SL) have been obtained at 13 stations where catches ranged up to 275 individuals per haul. An analysis of dispersion for this species (Struhsaker, 1973) shows it to have a highly clumped distribution. The type of bottom in the area of capture is primarily muddy sand interspersed with patches of sponge, broken shell, and rubble. *Bothus thompsoni* was often taken with 20-30 other species of fishes; it usually comprised less than 8% of the total catch, but occasionally ranged up to 30%. Numerically dominant species taken with *B. thompsoni* include *Trachinocephalus myops, Priacanthus* spp., *Antigonia eos, Parupeneus chrysonemus,* and *Lagocephalus hypselogeneion.* Struhsaker and Higgins (manuscr.[2]) have shown that *B. thompsoni* is the third most abundant larval flatfish (after *Engyprosopon xenandrus* Gilbert and *B. pantherinus)* taken in offshore midwater hauls near Oahu. They also presented evidence that *B. thompsoni* may spawn throughout the year.

ACKNOWLEDGMENTS

We thank John E. Randall for the photographs used in Figures 1 and 2 and for reviewing the manuscript. We are also indebted to Elbert H. Ahlstrom and C. Richard Robins for comments on the manuscript. The NMFS Systematics Laboratory provided the radiographs. The illustrations are by Tamotsu Nakata and Robert Bonifacio.

MATERIAL EXAMINED

USNM 208494: TC-33-52 (R/V *Townsend Cromwell*, cruise 33, station 52); 1 male (109.2 mm SL); lat. 19°58.3′ N, long. 156°28.5′ W; depth 72 m, 13 Nov. 1967. USNM 208495: TC-36-15; 4 females (93.7-99.1 mm SL); lat. 21°37.7′ N, long. 158°08.8′ W; depth 113 m, 2 May 1968. USNM 208496: TC-36-20; 7 females (39.5-72.8 mm SL), 12 males (55.8-81.2 mm SL); lat. 21°36.8′ N, long. 158°12.5′ W; depth 110 m, 3 May 1968. USNM 208497: TC-40-115; 10 females (56.9-87.3 mm SL), 5 males (70.0-84.5 mm SL); lat. 21°36.8′ N, long. 158°08.2′ W; depth 102 m, 8 Nov. 1968. USNM 208498: TC-40-116; 4 females (56.0-105.4 mm SL), 3 males (58.6-104.5 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 112 m, 1 Dec. 1968. USNM 208499: TC-40-119; 5 females (78.6-91.2 mm SL), 7 males (86.2-99.2 mm SL); lat. 21°36.8′ N, long. 158°11.2′ W; depth 96 m, 1 Dec. 1968. BPBM 14102: TC-40-125; 1 female (106.4 mm SL), 1 male (114.4 mm SL); lat. 21°36.8′ N, long. 158°11.6′ W; depth 102 m, 10 Nov. 1968.

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[2] Struhsaker, P., and B. E. Higgins. Unpubl. manuscr. Post-larval flatfishes (Pisces:Pleuronectiformes): Observations on the identity and ecology of 11 Hawaiian species. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.

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Laboratory Studies of Predation by Euphausiid Shrimps on Fish Larvae

G. H. Theilacker and R. Lasker

INTRODUCTION

Despite a large literature on the vulnerability of marine fish larvae to changes in their physical and biotic environment, there is surprisingly little quantitative data available on organisms that eat fish larvae. There is ample evidence that huge mortalities of yolk-sac fish larvae occur (Ahlstrom, 1965); this is not due to lack of food, a factor implicated in the mortality of older larvae (Blaxter, 1969). Predation on yolk-sac larvae may be the most important cause of mortality during the early period in the life history of pelagic fish. There are a number of observations of zooplankters feeding on fish larvae (Garstang, 1900; Lebour, 1925; Wickstead, 1965; Petipa, 1965; Fraser, 1969); copepods, chaetognaths, ctenophores, and a variety of coelenterates have been seen to capture and ingest marine fish larvae. Recently Lillelund and Lasker (1971) quantified the predator-prey relationship between several species of marine copepods and larvae of the northern anchovy, *Engraulis mordax*, and described the behavioural responses involved in this interaction. They found, for example, that a variety of marine copepods (but particularly surface-dwelling pontellids) can capture and ingest or fatally injure young anchovy larvae under laboratory conditions.

Our experiments were designed to determine whether euphausiids could capture fish larvae, and if so, how many and under what conditions. We have combined our laboratory findings with the field data given by Brinton (1967 and unpublished) to estimate the mortality of northern anchovy larvae that may be caused by co-occurring *E. pacifica*.

Of the oceanic zooplankters which frequent the upper mixed layer of the sea where fish larvae are found in greatest abundance, the euphausiid shrimps are often dominant in biomass and number, particularly during the night hours when they migrate to the surface. Although neither Ponomareva (1963) nor Mauchline and Fisher (1969), in their respective monographs, mention fish larvae as a food of euphausiids, most euphausiids are known to be omnivorous and capable of capturing zooplankters, e.g. chaetognaths and copepods; therefore fish larvae may be captured too. The fragile nature of most fish larvae and the lack of hard parts would make recognition of the remains impossible in the euphausiid intestine even if they were an important part of their diet.

Brinton (1962 and unpublished) has estimated the distribution and density of several euphausiid species in the California Current over a number of years, *Euphausia pacifica* Hansen being one of the most abundant species. The general feeding habits and ubiquity of *E. pacifica* in the California Current, and the fact that it can be maintained in the laboratory (Lasker and Theilacker, 1965; Lasker, 1966) prompted us to investigate it as a possible predator of marine fish larvae, particularly of the northern anchovy (*Engraulis mordax* Girard), the dominant clupeid fish in the California Current and to estimate larval mortality from field data.

METHODS

We collected euphausiids by towing a 1-m (mouth-diameter, 0.505 mm mesh) plankton net or a 60 cm diameter Bongo net without bridles with the same mesh size (McGowan and Brown, 1966) in the Pacific Ocean near San Diego and Santa Catalina Island, California, during the spring and summer of 1971 and 1972. On board ship euphausiids were separated from other plankton immediately and after allowing for the initial mortality of damaged animals (10-12 h), the survivors were kept separately in individual containers. Detailed methods for collecting and maintaining euphausiids are given by Lasker and Theilacker (1965).

Juvenile *E. pacifica*, ranging in total length from 6-10 mm and 0.6 - 2.1 mg dry weight, were caught most frequently. Some euphausiids were used for predation experiments on shipboard while others were brought back to the Southwest Fisheries Center aquarium, and used for as long as 25 days. When an experiment was terminated, each animal was measured, rinsed in distilled water, dried at 60°C, and weighed. The anchovy larvae fed to euphausiids were hatched from eggs collected from a spawning school in our aquarium facilities or from hormone-injected anchovies (Leong, 1971). For shipboard experiments the eggs were transferred from the aquarium to the ship, thus eliminating the need for catching anchovy eggs in net tows and sorting the eggs from other plankton.

Temperature was maintained at 17°C, close to the sea-surface temperature at the time euphausiids were captured. *E. pacifica* follows a low intensity light level of about 1×10^{-4} μW/cm^2 (Clarke, 1966) during vertical migration; we therefore performed all of our experiments in the dark. Unless otherwise noted, each feeding test lasted for 22 h with a euphausiid in 3500 ml sea water filtered earlier through a Cuno® Aqua Pure Filter (pore size 5 μ). In all experiments the young anchovy larvae appeared to be randomly distributed in the feeding containers.

FEEDING BY ADULT, JUVENILE, AND LARVAL *E. PACIFICA* ON LARVAL ANCHOVIES

Experiments were performed to compare the relative ability of different growth stages of euphausiids to capture anchovy larvae. Larval *E. pacifica* weigh less than 0.6 mg dry weight and are less than 6 mm in total length. Juveniles range from 0.6 - 2.1 mg and from 6 mm to slightly less than 11 mm in length; adults are 11 mm or more long and greater than 2.1 mg in weight (lengths from Brinton, personal communication). In these experiments the smallest *E. pacifica* tested was 5 mm long (0.15 mg) and the largest 20 mm (13.2 mg). The length range of *E. pacifica* in the California Current is from 1-21 mm.

Sixteen larval, 30 juvenile, and 27 adult *E. pacifica* were tested individually to determine their ability to feed on yolk-sac anchovy larvae. Larval and juvenile euphausiids were offered 20 anchovy larvae a day and adults were given 50-80 larvae per day in 3500 ml. Larval euphausiids ate a median number of 2 larvae/day (range 1-5), juveniles ate a median of 7 larvae/day (range 1-19), and adults ate a median of 17 larvae/day (range 5-38) (Fig. 1).

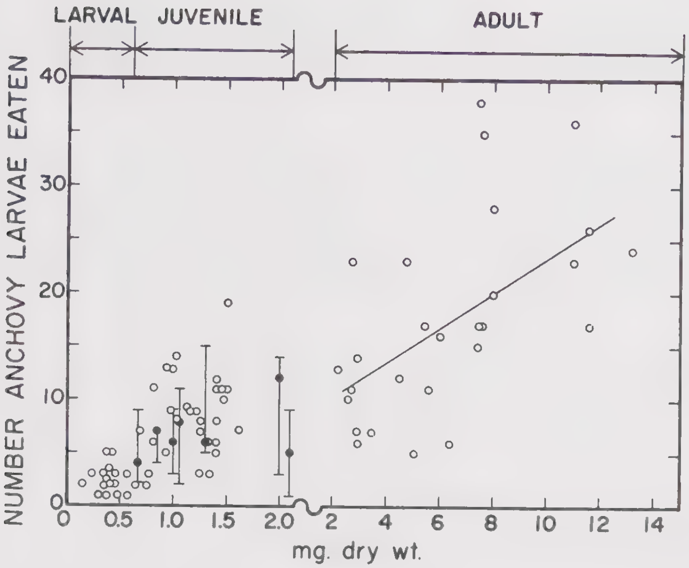

Fig. 1. Number of anchovy eaten per day by individual larval, juvenile, and adult *E. pacifica* (open circles). Closed circles indicate the median number of anchovy larvae eaten (with extremes given by the solid lines) when 7 individuals were fed daily for 5 consecutive days

No weight-specific feeding rate could be demonstrated within the juvenile size class (the slope [b = 4.07] does not differ significantly from zero [$p > 0.1$]). However, within the adult size group, feeding did increase with increasing animal size (Fig. 1). The slope (b = 1.69) of a least squares fit of the data differs significantly from zero ($p < 0.01$).

To test further the hypothesis that animal size, within the juvenile group, does not influence feeding, 7 juveniles were fed 20 anchovy larvae/day on each of 5 successive days. The euphausiids ranged from 7-11 mm (0.67 - 2.1 mg). The median number of anchovy larvae eaten per individual euphausiid/day ranged from 4-12 (Fig. 1). No significant difference in feeding could be demonstrated ($p > 0.20$) when the number of anchovy larvae eaten each day per animal was ranked and compared (Friedman two-way analysis of variance). All succeeding experiments were conducted with juvenile *E. pacifica*, since animal size did not influence feeding.

Lasker (1966) determined the carbon requirement at 10°C needed by various size groups of *E. pacifica* for growth, molting, respiration, and digestive inefficiency. From these data we calculated the necessary number of anchovy larvae which had to be consumed to satisfy the carbon requirement of larval, juvenile, and adult *E. pacifica*. Early anchovy larvae[1] weigh 22 μg and contain 42% carbon; therefore, one larva provides about 9 μg of organic carbon. If no other food is available the carbon requirements of larval euphausiids at 10°C can be satisfied if each eats 1 anchovy larva/day; juveniles require 3-5 larvae/day, and adults from 7-28 larvae/day, depending on the euphausiid's weight.

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[1] Lillelund and Lasker (1971, p. 664) gave 10 μg for the dry weight of a yolk-sac anchovy larva. This figure should have been 22 μg.

At 17°C, the temperature of these experiments, the carbon requirements for growth, molting, and respiration would be greater than at 10°C. Respiratory carbon losses at 17°C are increased by 60% ($Q_{10} = 2$; Lasker, 1960) over the losses at 10°C and since respiration alone accounts for most of *E. pacifica's* total carbon requirement (Lasker, 1966) we adjusted the above anchovy larval carbon equivalents by 60%. This increases the larval euphausiids daily requirement, see Table 1.

Table 1. The number of anchovy larvae/day needed by larval, juvenile, and adult *E. pacifica* to satisfy their daily carbon requirements at 17°C (based on Lasker, 1960, 1966) compared to the median and maximum number of anchovy larvae eaten by euphausiids in laboratory experiments

E. pacifica	Anchovy larvae required/day	Anchovy larvae eaten	
		Median	Maximum
Larval	1-2	2	5
Juvenile	5-8	7	19
Adult	11-45	17	38

FEEDING AT DIFFERENT PREY CONCENTRATIONS

The quantity of prey offered to juvenile euphausiids was varied from 1-80 anchovy larvae per 3500 ml/day. When 10 or less larvae were fed to juvenile euphausiids the maximum number eaten (Fig. 2) appears to be limited by the number fed and, probably, the searching capability of the euphausiid. Increasing the density further, offering more than 10 larvae, did not cause any differences in the median feeding rate. Feeding rates were compared statistically at 3 food concentrations (Fig. 2) 18-21, 29-32, and 40-50 larvae fed per container. The median number eaten per day increased from 6 at the lowest density (20 observations), to 8 at the next (9 experiments) and 10 at the highest density (6 experiments); however, no differences could be demonstrated between each paired comparison (Mann-Whitney U test, $p > 0.20$ for each pair tested).

From these experiments it appears that the average number of anchovy larvae juvenile euphausiids can process in a day - catching, eating, digesting, and excreting - is 10 or less. Increasing the prey concentration above this number had no effect on feeding in the volumes tested. This independence between feeding and food concentration has also been described for the crustacean *Daphnia* (Rigler, 1961) and the chaetognath, *Sagitta* (Reeve, 1964). Both authors found that above a critical food concentration the food-intake rate held constant as the food density continued to increase.

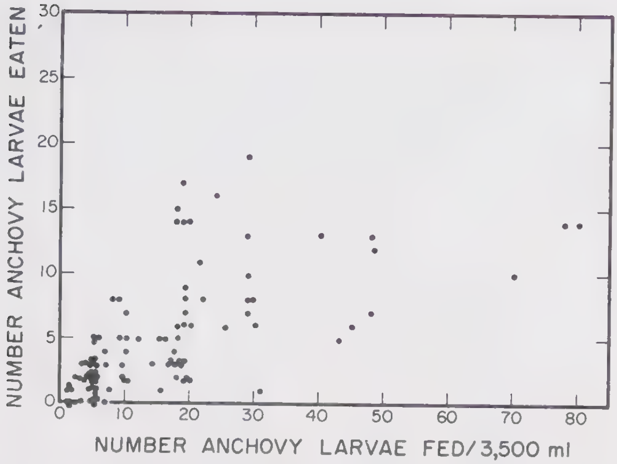

Fig. 2. Feeding of juvenile *E. pacifica* at different concentrations of anchovy larvae

FEEDING RATE

Fisher and Goldie (1959), studying the euphausiid *Meganyctiphanes norvegica*, did not find consistent differences in the amount of feeding between day and night samples taken in the North Sea. However, Ponomareva (1954) found that *E. pacifica* fed at a higher intensity during the evening and night in the Sea of Japan. Roger (1971) also observed a feeding rhythm for most of the 28 euphausiid species he studied in the field. He noted that the intensity of feeding usually increased before the nocturnal ascent, so that the rhythm was not, in most cases, synchronous with the day-night vertical migration.

Feeding intensity may be correlated only with the availability of food. To determine whether a periodicity in *E. pacifica* feeding could be demonstrated when food is not limiting, 11 juvenile euphausiids were fed anchovy larvae for 3 consecutive 12-h periods (midnight and noon were chosen as starting times to avoid any effect of a diel rhythm). Twenty larvae were offered to each euphausiid at the beginning of each 12-h experiment. At the end of the 36-h period, the animals were fed 20 larvae for 24 h. The median number of larvae eaten was 2 (Table 2) during the first 12 h (noon to midnight); 4 were eaten in the midnight-to-noon period and 2 in the second non-to-midnight period. The median for the 24-h period was 5. No periodicity in feeding can be shown when the data were tested statistically. Feeding during the three 12-h periods was homogeneous when compared using Friedman's two-way analysis of variance by ranks ($p > 0.20$). Also, no differences could be demonstrated by comparing the 2 combined noon-midnight periods with the midnight-noon period (Mann-Whitney U, $p = 0.68$). The results suggest a constant feeding rate when food is not a limiting factor.

Table 2. The number of anchovy larvae eaten by 11 juvenile *E. pacifica* for each of 3 consecutive 12-h feeding periods followed by a 24-h period

Juvenile *E. pacifica* mg dry weight	Noon-midnight 12 h	Midnight-noon 12 h	Noon-midnight 12 h	24 h
2.00	8	4	8	3
2.10	5	0	2	1
0.52	0	6	6	5
1.28	1	4	3	5
1.23	2	5	3	7
0.67	3	4	6	4
0.56	0	2	0	1
0.82	3	2	2	7
1.00	2	4	1	6
0.84	1	0	0	4
1.02	1	2	2	5
Median number eaten	2	4	2	5

EFFECT OF TIME IN CAPTIVITY ON FEEDING BY JUVENILE *E. PACIFICA*

Twelve animals (0.5 - 2.1 mg dry weight) tested aboard ship on the first day of capture ate a median of 6.5 anchovy larvae when 18-20 were offered in 3500 ml, consuming between 2-13 larvae individually. Eight other juveniles (0.7 - 2.0 mg dry weight) were observed in the laboratory to determine whether or not feeding rate changed during captivity. Five days of feeding (7, 8, 13, 17, and 21 days after capture), when the density of larvae offered was the same as in the above shipboard experiments, were compared (Table 3). The number of larvae eaten per animal on each day was ranked. The sums of the daily ranks were compared and no significant difference in feeding rates was obtained (Friedman two-way analysis of variance by ranks, $0.1 < p < 0.2$). The number of larvae eaten by all animals varied from 1-15 per day; the individual medians for the 5 days of feeding ranged between 2 and 12 and the overall median number of larvae eaten was 6. Therefore, the daily feeding rate of juvenile *E. pacifica* does not appear to change with the time maintained in captivity.

Table 3. Feeding by 8 juvenile *E. pacifica* maintained on anchovy larvae in the laboratory for 3 weeks

Juvenile E. pacifica	Number of anchovy larvae eaten					
	Days after capture					Median
	7	8	13	17	21	
no. 1	5	5	8	15	6	6
2	12	3	14	4	14	12
3	7	1	8	3	9	7
4	6	4	2	3	9	4
5	4	7	5	7	7	7
6	1	4	3	1	2	2
7	4	6	3	9	9	6
8	3	5	11	8	8	8

THE EFFECT OF AN ALTERNATIVE PREY

Lillelund and Lasker (1971), in their study on the predation of anchovy larvae by the copepod *Labidocera trispinosa,* found that the addition of *Artemia* nauplii, as an alternate prey, decreased the feeding on larvae. The decrease in feeding rate was proportional to the density of the additional prey; at high nauplii densities fewer larvae were killed. *Euphausia pacifica* will also feed on *Artemia* nauplii, the number eaten determined by Lasker (1966) being 100-350/day for *E. pacifica* ranging in dry weight between 1.8 and 5.6 mg. Nine individual juvenile *E. pacifica* were offered 20 larvae daily for 5 consecutive days with *Artemia* nauplii as an alternative. Four of the experiments were conducted in 3500 ml and 5 in 700 ml containers. On the 2nd, 3rd, and 4th days *Artemia* nauplii were also given at densities of one nauplius per 5, 10, 20, and 40 ml. The median number of the larvae eaten in the 3500 ml containers was 5 when anchovy larvae only were offered, but 3 when *Artemia* nauplii were present with the larvae; in the 700 ml containers the median number eaten was 5 for each treatment. The data were tested statistically (the 2 container sizes tested separately) by comparing the ranked sum of the number of anchovy larvae eaten for the 3 days when *Artemia* were present to the number eaten during the 2 days when anchovy larvae alone were fed. The ratio of the sums of the ranks for the 2 treatments (with and without *Artemia* nauplii) was the same as the ratio of the number of observations (for both container volumes), so the null hypothesis must be accepted ($p > 0.20$, Mann-Whitney U Test).

The same data were rearranged to test the daily feeding on anchovy larvae as a function of *Artemia* density (Fig. 3). The data were homogeneous; feeding on larvae was the same at each *Artemia* density (Friedman's two-way analysis of variance by ranks, $p > 0.20$). Therefore, the presence of *Artemia* nauplii, even at a density of one per 5 ml, does not alter euphausiid feeding on anchovy larvae.

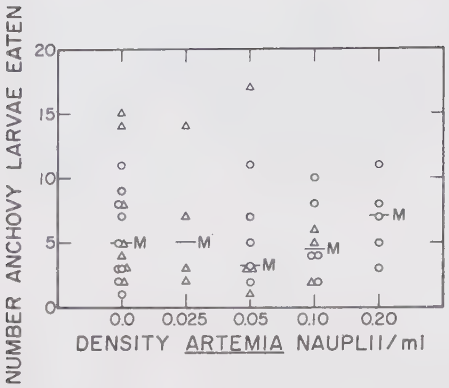

Fig. 3. Predation by *E. pacifica* on anchovy larvae with addition of *Artemia* nauplii as an alternative prey. o = 3500 ml container; △ = 700 ml container; M = median number during control and at each *Artemia* density

In all of the experiments in which *Artemia* nauplii were offered, the number of nauplii eaten increased as the nauplii concentration was increased. Filtering rates (Gauld, 1951) calculated from the number of nauplii eaten at each density remained constant (Friedman's two-way analysis of variance by ranks, $p > 0.20$), indicating that the *Artemia* are filtered as a passive particle. Brooks (1970) concluded that particle-feeding copepods grazed on *Artemia* as a passive particle and that predatory copepods may feed on *Artemia* nauplii in preference to natural nauplii only because they are more easily captured and no active selection of the *Artemia* nauplii over the natural nauplii is involved.

STARVATION

Several juvenile euphausiids, 0.6 - 0.8 mg dry weight, were kept in the laboratory for 24 days without feeding. These animals commenced feeding on anchovy larvae and molted for 2 additional weeks when the experiment was terminated.

To determine whether or not periods of starvation cause a change in feeding rate, 8 individual juvenile *E. pacifica*, (0.70 - 2.00 mg dry weight) were either fed 20 larvae/day on consecutive days or starved from 2-3 days and then fed 20 larvae. Each individual (9-10 observations/animal) was tested separately, comparing the number of larvae eaten during a day of feeding when the animal had been fed the previous day to the number eaten when the animal had not been fed the previous day. One euphausiid ate less than usual after a period of starvation ($p < 0.05$); however, the other 7 animals showed no differences in the daily feeding patterns whether or not the euphausiids had fed the previous day (p values all >0.20, Mann-Whitney U Test). Therefore, under laboratory conditions, when food is not limiting, 2-3 days of previous starvation does not appear to have an effect on feeding.

MOLTING

Lasker (1966) found that molting of *E. pacifica* depressed the feeding on *Artemia* nauplii. To test for this effect, the data from all the anchovy larvae feeding experiments were combined and the number eaten on days the euphausiids did and did not molt were compared. Juvenile euphausiids used in this comparison were fed more than 10 larvae/day and had molted at least once. The median number of larvae eaten for 99 animal-days when the euphausiid did not molt was 7 (range 1-19). There were only 11 molting days that fit the above requirements. The median number of larvae eaten during a molting day was 5 (range 1-14). No significant difference could be demonstrated between the 2 sets of data (Mann-Whitney U Test $p = 0.63$); hence molting does not appear to depress the feeding of *E. pacifica* on anchovy larvae.

The median intermolt period at 17°C for *E. pacifica* fed anchovy larvae (22 observations on 12 animals) was 4 days, the range was between 2 and 6 days; 91% of the observations were between 3 and 5 days. This is the same molting frequency observed by Lasker (1966) for *E. pacifica* fed *Artemia* nauplii at 15°C.

FEEDING ON OLDER ANCHOVY LARVAE

Lillelund and Lasker (1971) noted in their predation study that the ability of the copepod *Labidocera trispinosa* to capture anchovy larvae decreased as the larvae aged and became more active. A 1-day-old anchovy larva rests more than 95% of the time and 2-day-old larvae rest about 70% of the time; at 3 days of age the larva spends almost 50% of its time in intermittent swimming and the next day swims intermittently 85% of the time (Hunter, 1972). Increasing larval activity correlates well with the decreasing ability of *E. pacifica* to capture larval anchovies.

Day-1 (newly hatched) and 2-day-old larvae were fed to 10 individual juvenile euphausiids at a concentration of 1 larva/3500 ml. In this situation the euphausiids were 60% successful in capturing the single larva. Successful capture dropped to 17% when the larvae were 3 days old (12 experiments) and to 11% for 4-day-old larvae (9 experiments), all fed to the euphausiids at the same low density.

FEEDING ON ANCHOVY EGGS

E. pacifica will feed on anchovy eggs although the incidence of ingestion is very low in the laboratory. This is probably because the eggs are unavailable to the euphausiid, floating at the surface of the sea water since there was no water movement in the containers. In the open ocean, anchovy eggs are distributed in the upper 50 m of the water column (Ahlstrom, 1959).

Sixteen juvenile euphausiids were offered 20 anchovy eggs each in 700 ml. Only 3 animals ate eggs; the median number eaten was 5.

CO-OCCURRENCE OF *E. PACIFICA* AND ANCHOVY LARVAE IN THE CALIFORNIA CURRENT

Dr. Edward Brinton of SIO has kindly provided us with unpublished data on the abundance of *E. pacifica* in the California Current. The euphausiids were collected in standard (1-m net towed to 140 m depth) night CalCOFI tows (Kramer et al., 1972) between January 1953 and July 1955. The counts are given as numbers of individuals/1000 m^3 of each mm size group, 1-21 mm, per station per month for 27 stations between Point Conception and San Diego (Fig. 4), an area of 30,000 square miles (8 X 10^{10} m^2).

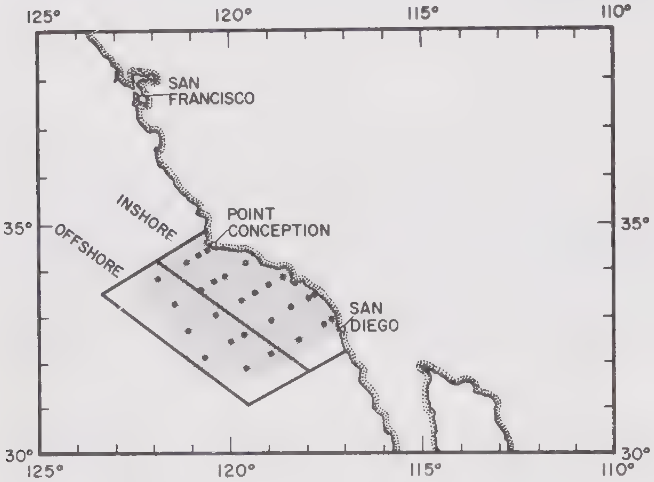

Fig. 4. Map showing anchovy (outlined) and euphausiid (shaded) surveys. ● = euphausiid stations

The abundance of anchovy eggs and larvae in the California Current has been studied intensively since 1949. Data for the anchovy spawning season during 1953, 1954, and 1955 in the same area of the California Current as Brinton's euphausiid study are given by Smith (1972). The anchovy area extends 40 miles further south than the euphausiid area (Fig. 4). Spawning during the 1953-1954 season was between October 1953 and March 1954; in 1955 the major spawning was in the first quarter of the year and is given in numbers of anchovy larvae per m^2 sea surface per positive station in Table 4. There were more positive stations inshore (to 80 miles off the coast) than offshore (between 80 and 160 miles off the coast); the frequencies are given in Table 4. Although there is some spawning throughout the year, the number of larval anchovies is only one-tenth to one-fourth of the number obtained during peak spawning. During the spawning period 68% of the larvae sampled were 5.25 mm or less in length (Smith, personal communication), or between hatching and 1-week-old.

About 98% of the anchovy larvae occur above 56 m and 49% are above 8 m (Ahlstrom, 1959). The vertical distribution of each *E. pacifica* size group was calculated from data provided by Brinton (unpublished and 1967). The samples, taken at 25-m increments between 25 and 250 m with a closing net, were collected at 4 night stations. Night catches indicate that an average of 87% of larval, juvenile, and adult *E. pacifica* are above 50 m. However, because of active vertical migration it is conceivable that all of the euphausiids may reach the surface some time during the night.

Table 4. The estimated number of anchovy larvae (<5.25 mm long) under 1 m^2 of sea surface during the peak spawning season in 1953, 1954, and 1955

Spawning season	Inshore		Offshore	
	No. larvae/m^2	No. positive stations	No. m^2	No. positive stations
1953	36	100	13	86
1954	59	100	11	83
1955	38	95	4	69

The average number of larval, juvenile, and adult *E. pacifica* under 1 m^2 of sea surface in the area of the California Current is tabulated in Table 5 for the months of peak anchovy spawning in 1953, 1954, and 1955 (9 months). At the median feeding rates on anchovy larvae determined in this study and the mean euphausiid densities calculated to include the number of euphausiids co-occurring with anchovy larvae, 831 anchovy larvae could be consumed/day/m^2. For the purpose of this discussion we assume that *E. pacifica* is in the upper 50 m of the water column for 10 h, an hour after sunset to an hour before sunrise. If the total water column *E. pacifica* frequents daily is considered, the *E. pacifica* (average of Brinton's 29-month survey) under 1 m^2 of sea surface could devour a total of 2847 fish larvae/day/m^2 (Table 5) regardless of other zooplankton being present.

Table 5. The average number of *E. pacifica* under 1 m^2 sea surface and the total number of fish larvae that could be consumed daily

	Larval	Juvenile	Adult	Total
No. of *E. pacifica*/m^2 during peak anchovy spawning (9 mo. average)	314	118	38	470
No. of *E. pacifica* above 50 m at night	273	103	33	409
No. of fish larvae *E. pacifica* above 50 m can consume/10 h/m^2	248	328	255	831
E. pacifica /m^2 (29 mo. average)	582	139	43	764
No. of fish larvae *E. pacifica* can consume/2 h/m^2	1,164	952	731	2,847

It is possible that the small number ($<60/m^2$) of anchovy larvae caught in plankton nets (Table 4) is a result of heavy predation. The abundance of euphausiids and other predators may be a factor in determining the patchiness of fish larvae.

SUMMARY

The abundant euphausiid in the California Current, *Euphausia pacifica*, may be an important predator of fish larvae. Laboratory experiments showed that when the number of yolk-sac anchovy larvae (*Engraulis mordax*) offered was not limiting (not less than one larva/350 ml) the median number eaten per day by larval *E. pacifica* was 2; juvenile euphausiids eat 7, and adults 17. The carbon requirements of *E. pacifica* for the 3 growth stages is approximately the amount of carbon provided by the median feeding rates. Within the adult euphausiid size group, feeding on fish larvae significantly increased with increasing animal size, but no size-specific feeding could be demonstrated for juvenile euphausiids. All replicate experiments with individual *E. pacifica* in this study were conducted with juveniles. These showed that the amount of feeding was not affected by the addition of another prey, imposed starvation, molting, or the length of time the euphausiids were in captivity. The amount of feeding increased as the prey density was increased from 1-10 larvae offered per 3.5 l/day; further increases had no effect. Feeding rate was constant regardless of time of day. The percent capture of fish larvae by euphausiids was lower than usual when older, more active anchovy larvae were offered. These studies are discussed in terms of field data collected in the area of the California Current where *E. pacifica* and anchovy larvae co-occur.

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Maturation and Fecundity of Swordfish, *Xiphias gladius,* from Hawaiian Waters

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ABSTRACT

Sixteen swordfish, *Xiphias gladius*, ovaries ranging in weight from 39 to 20,000 g were examined. Fish size ranged from 47 to 246 kg. Based on the occurrence of ripe ovaries, spawning in Hawaiian waters was estimated to extend from April through July. The developmental stages of ova are described; the most advanced ova examined averaged 1.6 mm in diameter. The distribution of ova diameters within an ovary was found to be heterogeneous. Fecundity was estimated for eight swordfish. Some variability in fecundity was noted; a positive curvilinear relationship of increase in fecundity with increase in fish size was evident. Best estimates suggest that an 80 kg swordfish has 3.0 million ova (early ripe or ripe stages) and a 200 kg swordfish has 6.2 million ova.

The occurrence in Hawaiian waters of mature swordfish, *Xiphias gladius,* with ovaries in advanced stages of maturation has been observed in the past by longline fishermen and other members of the fishing industry. However, precise information of the spawning period and the fecundity of swordfish from the Hawaiian Islands area is lacking. Although swordfish are not taken in large numbers by the longline fishery (Fig. 1), the absence of studies on swordfish has been due principally to difficulty in obtaining adequate data. The large ovaries of swordfish along with ovaries of other billfishes and tunas are commercially valuable and considered as a food delicacy in Hawaii. Thus, in order to prevent damage to the gonads, the auction firms handling the sale of swordfish do not permit the fish to be cut open prior to sale. Since fish are often butchered outside of the auction area, we were unable to obtain the needed information on sex and maturity. Although very little data on swordfish were available during our six years of sampling (1961-66), we were able to collect 16 ovaries covering all seasons of the year. These samples and related data on swordfish were considered adequate to permit us to make a preliminary assessment of spawning and fecundity of swordfish; the results are presented in this paper.

OCCURRENCE OF SWORDFISH IN HAWAIIAN WATERS

Swordfish are taken exclusively with longline fishing gear in Hawaiian waters. The swordfish catch landed by the Hawaiian fishery is very small; the total annual catch did not exceed 120 fish during the six years of sampling (Fig. 1). Since fishing for

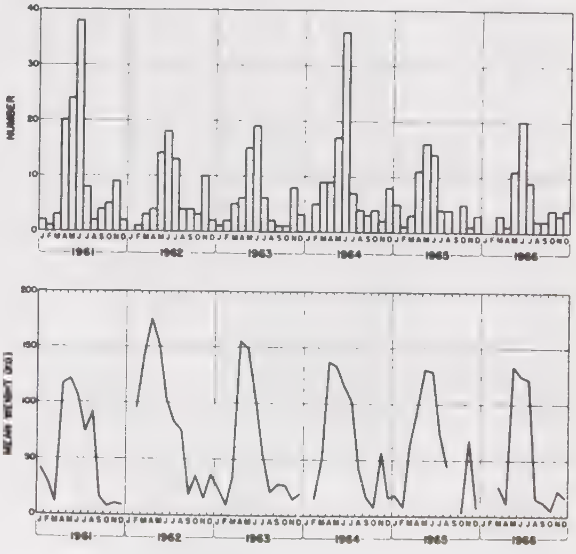

Figure 1.—Monthly landings of swordfish (upper panel) and average size of fish (lower panel) from 1961 to 1966.

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swordfish with longline gear is more successful during the night than day (Ueyanagi, 1974), the low catches may only be reflecting the fact that the Hawaiian fishery operates principally during daylight hours. Day fishing is carried out to maximize the catch of tunas and species of billfishes other than swordfish.

Figure 1 shows the monthly landings of swordfish for the period 1961-66. Although catches are small, there is a pronounced increase in landings during the summer months with the peak occurring in July. The increase is due to an increase in availability and not to an increase in fishing effort, since Yoshida (1974) showed that the catch rates (catch per trip) for blue marlin, *Makaira nigricans,* and striped marlin, *Tetrapterus audax,* in the Hawaiian longline fishery parallel the monthly landings, thus suggesting that the monthly catch data could be used as a general measure of availability.

The average size of swordfish also shows a peak during the summer period. As it will be discussed later, the increase in average size accompanied by the appearance of females in late stages of maturation may be related to a spawning migration.

MATERIALS AND METHODS

The 16 swordfish ovaries were collected at the Honolulu fish markets between June 1964 and May 1967 (Table 1). Since longline-caught fish are kept refrigerated with crushed ice, the ovaries were kept in an unfrozen condition until collected.

In the laboratory, excess connective tissue was removed from the external surfaces of the ovaries. The ovaries were weighed to the nearest gram and preserved in 10% Formalin. Detailed microscopic examination of the ovaries was undertaken only after the ovarian material had been thoroughly preserved, and shrinkage had stabilized. Generally, ova diameter measurements were taken after preservation had exceeded 6 mo.

For the maturation study, a small sample was extracted from the ovary with a cork borer and 100 randomly selected ova were measured to obtain mean diameter values for the most developed ova size group. Individual ova diameters obtained were not necessarily the maximum diameters. We followed the method developed by Yuen (1955) for measuring bigeye tuna ova and used by Otsu and

Table 1.—Summary of swordfish data used in maturation and fecundity study.

			Paired ovary weights			Most advanced mode			
Sample number	Date of landing	Fish size (kg)	Fresh (g)	Preserved in 10% Formalin (g)	Maturity[1]	Mean diameter (mm)	Number measured	Fecundity (millions of ova)	Gonad[2] index
BB-1	6/24/64	187.2	11,566	10,033	ER, RS	1.019	153	2.24	6.18
BB-2	6/25/64	121.5	10,205	6,805	RP	1.205	257	3.84	8.40
BB-3	6/25/64	204.1	19,958	19,609	RP, RS	1.364	172	6.18	9.78
BB-4	7/ 3/64	156.5	9,389	(8,267)[3]	ER	0.986	228	4.80	6.00
BB-5	7/ 3/64	142.4	8,373	(7,332)[3]	ER	0.923	403	9.38	5.88
BB-6	7/ 6/64	246.3	1,542	1,430	ED, RS	0.101	100	—	0.63
BB-7	7/17/64	86.6	184	169	IM	0.060	100	—	0.22
BB-8	11/26/65	17.7	39	39	IM	0.057	100	—	0.22
BB-9	1/ 2/66	68.0	508	490	ED	0.141	100	—	0.75
BB-10	1/25/67	90.3	390	415	ED	0.154	100	—	0.43
BB-11	2/24/67	46.7	(Damaged)						
BB-12	4/ 5/67	54.4	172	174	ED	0.107	100	—	0.32
BB-13	4/13/67	76.6	163	176	IM	(poorly preserved)			0.21
BB-14	4/27/67	121.5	8,164	(7,187)[3]	RP	1.438[4]	113	3.73	6.72
BB-15	5/22/67	83.0	4,327	4,200	ER	0.990	306	3.21	5.21
BB-16	5/28/67	202.7	8,255	8,197	ER, RS	1.033	296	6.54	4.07

[1] Key: IM - Immature
ED - Early developing
ER - Early ripe
RP - Ripe
RS - Residual eggs present

[2] Gonad index is percentage of fresh ovary weight to fish size.

[3] Weight estimated from fresh-preserved conversion given in Figure 2.

[4] Ova diameters of fresh (non-preserved) samples placed in sea water averaged 1.571 mm.

Uchida (1959) for albacore. The measurement was the random diameter located parallel to the ruled lines marked on the measuring dish.

For ovaries in the early ripe or ripe stages, ova diameters were taken to obtain the mean diameter of the most advanced mode. A small sample of the ovarian tissue was extracted with a cork borer from the area near the lumen of the posterior region of the right ovary. Excess liquid was first blotted out and the sample weighed on an analytical balance. All ova in the most advanced stage were measured and counted, the latter to obtain fecundity estimates.

Weights of preserved ovaries from four fish were not recorded (Table 1). Since three of these samples were in the early ripe or ripe stages of maturity and could be used for fecundity estimates, we computed a conversion factor to correct for shrinkage due to preservation. Figure 2 shows the regression of fresh whole ovary weight on preserved (10% Formalin) ovary weight. The regression computed on the transformed data ($\log_e$) shows a very good fit for the 12 sets of data. The equation was used to estimate the preserved weights of the three samples (Table 1).

Sample BB-3 (Table 1) was used to test for homogeneity of ova diameters within a pair of ovaries. A cork borer (14.29 mm diameter) was used to obtain a core sample which extended from the outer surface of the ovary to the centrally-located lumen. The core was divided into an outer layer, a central layer located next to the lumen, and a middle layer. Separate cores were taken from the anterior, middle, and posterior region of both ovaries, thus providing a total of 18 subsamples. Ripe ova were teased from each sample and 200 randomly-selected ova were measured

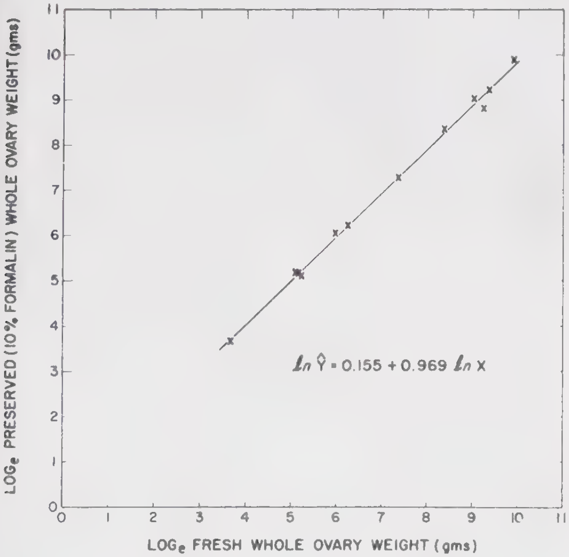

Figure 2.—Relationship of fresh ovary weight to preserved (10% Formalin) ovary weight for swordfish.

DEVELOPMENTAL STAGES OF OVA

An examination of the physical appearance of ova from swordfish showed that the ova could be classified easily into several developmental stages which were not dependent on ova diameters. The stages are described as follows:

1. Primordial Ova
   Ova are transparent, ovoid in shape, and diameters range from 0.01 to 0.05 mm. Primordial ova are present in all ovaries.
2. Early Developing Ova
   Ova are still transparent and ovoid in shape; diameters range from approximately 0.06 to 0.24 mm. A chorion membrane has developed around the ovum and an opaque yolk-like material has begun to be deposited within the ovum.
3. Developing Ova (Figure 3A)
   Ova are completely opaque, more wedge-shaped than ovoid, and diameters range between 0.16 to 0.96 mm. The chorion is stretched and not visible in this stage.
4. Advanced Developing Ova (Figure 3B)
   Ova are ovoid and diameters range from 0.47 to 1.20 mm. Ova have a translucent margin, a fertilization membrane, and a round yolk.
5. Early Ripe Ova (Figure 3C)
   Ova diameters range from 0.60 to 1.20 mm. The yolk material is translucent and oil globules have begun to form.
6. Ripe Ova (Figure 3D)
   Ova are transparent and with oil globules. Diameters range from 0.80 to 1.66 mm.
7. Residual Ova
   Ova in this stage show signs of degeneration. Ova are thin-walled and translucent and have shrunken and measure approximately 0.80 mm in diameter.

HETEROGENEITY OF OVA DIAMETERS

The distribution of ova diameters in sample BB-3 was examined critically to test for heterogeneity. A chi-square test of the normality of the size frequency distribution of ova diameters for the 18 samples (Appendix Table 1) showed significant differences for sample RMO ($P = 0.01$) and samples RMC and RPO ($P = 0.05$). An analysis of variance for one-way design was used to test for homogeneity (Table 2). The null hypothesis that the distribution of ripe ova was homogeneous throughout the ovaries was rejected ($P<0.05$; F ratio of 5.2821; *d.f.* 17 and 3,582). An examination of the means showed no general trends with the different sections of each ovary and locations within each section. The lack of homogeneity in ova has also been demonstrated for bigeye tuna (Yuen, 1955) and albacore (Otsu and Uchida, 1959).

A further evidence of heterogeneity was indicated in a comparison of ripe and early ripe ova. Table 3 shows the number of ripe and early ripe ova from the nine locations sampled from the right ovary. The ratio of ripe to early ripe ova ranged from 0.5576 to 2.6792. Three samples, RPC, RPM, and RMC, had almost identical ratios; but no consistent pattern was evident.

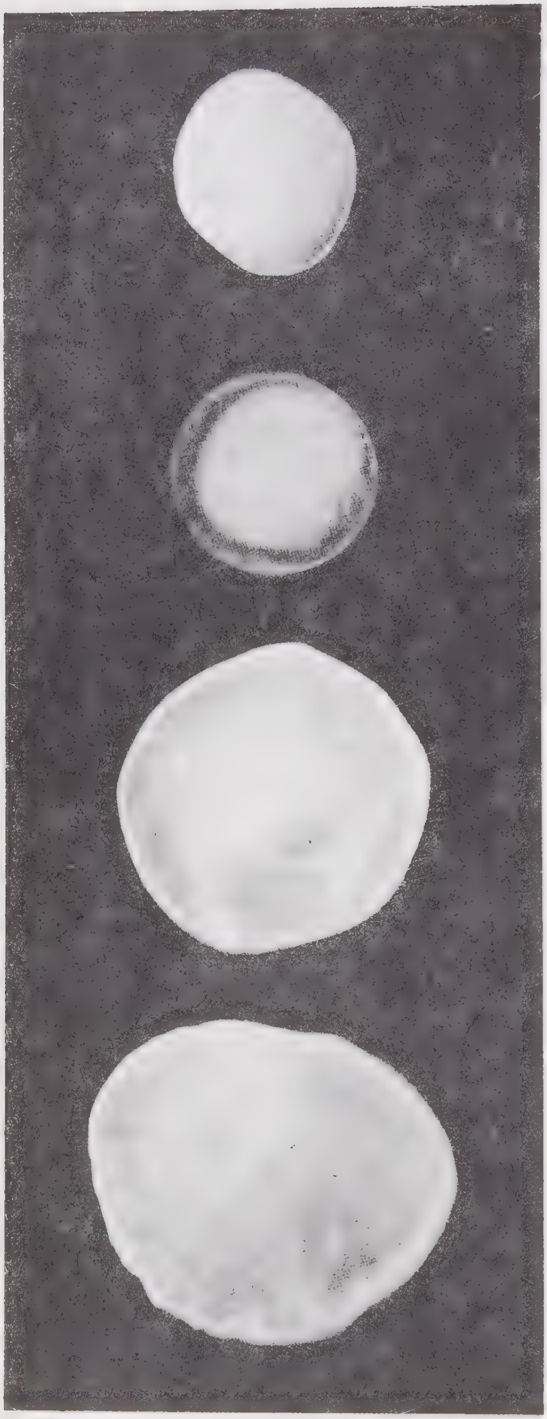

Figure 3.—Developmental stages of swordfish ova. **A.** Developing. **B.** Advanced developing. **C.** Early ripe. **D.** Ripe.

SPAWNING

Swordfish with ovaries in a ripe condition have been reported in the Mediterranean Sea off Sicily (Sella, 1911), in the Gulf Stream off Cuba (LaMonte, 1944) and in the western Pacific Ocean in the seas adjacent to Minami Tori Shima located at long. 156°E, lat. 25°17′N (Nakamura et al., 1951). Yabe et al. (1959) reported the occurrence of swordfish with ripe ovaries in the North Pacific Ocean in waters extending from the Subtropical Convergence to the equator and in the South Pacific in the Coral Sea and near the Fiji Islands. Yabe et al. (1959) also reported on the occurrence of seven ripe ovaries taken from swordfish caught in the Indian Ocean.

The appearance in April through July (Table 1) of large swordfish in the late stages of maturity suggests that the movement into coastal waters of the Hawaiian archipelago may be part of a spawning migration. Matsumoto and Kazama (1974) identified swordfish larvae from plankton hauls taken in Hawaiian waters, thus confirming the indirect evidence based on our ovary maturation study. Cavaliere (1962) reported that embryos start to form in eggs with diameters between 1.60 and 1.80 mm. In our samples the mean ova diameters of the most advanced modes of the preserved material were 1.20 mm for sample BB-2, 1.36 mm for BB-3, and 1.44 mm for BB-14. Ova from sample BB-14, which had been immersed in seawater prior to preservation, had a mean diameter of 1.57 mm. Since the gonad

Table 2.—Test of ova diameters from selected locations from right and left ovary of sample BB-3; analysis of variance for one-way design.

Treatment[1]	Sample size	Mean micrometer units	Standard deviation	Mean (mm)
RAC	200	69.38500	6.133913	1.4223
RAM	200	69.93500	6.480799	1.4336
RAO	200	68.41500	7.441750	1.4025
RMC	200	67.51500	7.646705	1.3840
RMM	200	67.51000	7.418561	1.3839
RMO	200	67.93500	8.098684	1.3926
RPC	200	69.44500	7.664900	1.4236
RPM	200	69.94000	7.077913	1.4337
RPO	200	72.00000	6.587639	1.4760
LAC	200	68.96500	6.347853	1.4137
LAM	200	69.97000	6.592144	1.4343
LAO	200	70.19000	6.296197	1.4388
LMC	200	69.86000	5.928416	1.4229
LMM	200	68.19500	6.523783	1.3979
LMO	200	69.48500	6.331683	1.4244
LPC	200	69.41000	5.725012	1.4229
LPM	200	69.40500	6.811972	1.4336
LPO	200	69.80000	5.445941	1.4309

Analysis of Variance

	Sum of squares	*d.f.*	Mean square	*F* ratio
Between groups	4072.5925	17	239.5643	5.2821
Within groups	162458.1074	3582	45.3540	
Total	166530.6992	3599		

[1] RAC - Right anterior center
RAM - Right anterior mid-layer
RAO - Right anterior outer layer
RMC - Right middle region center
RMM - Right middle region mid-layer
RMO - Right middle region outer layer
RPC - Right posterior region center
RPM - Right posterior region mid-layer
RPO - Right posterior region outer layer
LAC - Left anterior center
LAM - Left anterior mid-layer
LAO - Left anterior outer layer
LMC - Left middle region center
LMM - Left middle region mid-layer
LMO - Left middle region outer layer
LPC - Left posterior region center
LPM - Left posterior region mid-layer
LPO - Left posterior region outer layer

Table 3.—Ratio of numbers of ripe to early ripe ova.

Sample[1]	Number of early ripe ova	Number of ripe ova	Ratio index
RAC	170	212	1.2470
RAM	195	291	1.4923
RAO	220	256	1.1636
RMC	303	269	.8877
RMM	319	212	.6645
RMO	477	266	.5576
RPC	194	172	.8865
RPM	280	248	.8857
RPO	106	284	2.6792

[1] RAC - Right anterior center
RAM - Right anterior mid-layer
RAO - Right anterior outer layer
RMC - Right middle region center
RMM - Right middle region mid-layer
RMO - Right middle region outer layer
RPC - Right posterior region center
RPM - Right posterior region mid-layer
RPO - Right posterior region outer layer

index measures gonad size relative to fish size, it is not surprising to find that the highest gonad indices occurred during the apparent spawning period April to July (Table 1).

Since residual ova are remains from previous spawning (Yuen and June, 1957), all ovaries from our collection were examined for these ova. Residual ova were only evident in some of the samples collected in May, June, and July (Table 1). Although Yabe, et al. (1959), assumed that the ripe ova (modal diameter 1.2 mm to 1.6 mm) were spawned at one time, partial spawning of swordfish cannot be discounted as sample BB-3, which was judged ripe, also had residual ova.

It is interesting to note that Sella (1911) reported that the swordfish ovary contracts after spawning and remains compact and firm. This differs from tunas, which tend to be noticeably flaccid (Yuen, 1955). Sample BB-6, which was collected in July, appeared to confirm the general condition described for swordfish. Although this ovary was in an early stage of maturity and was firm and compact, it also contained residual ova, suggesting recent spawning.

No early ripe or ripe ovaries were collected from August to April. To some extent this feature may only reflect absence of mature fish, since nearly all of the swordfish taken during this period were small in size (Table 1) and indicative of immature fish.

FECUNDITY

Fecundity estimates are presented in Table 1 and shown in Figure 4. Since homogeneity tests showed significant differences in the distribution of ova diameters within a single pair of ovaries, the estimates should be considered only as rough approximations of the true fecundity of the swordfish. It

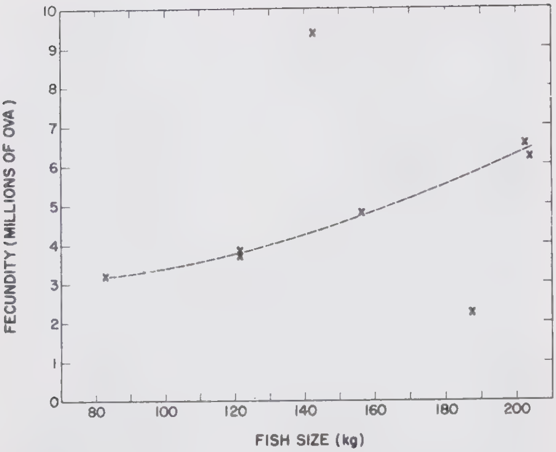

Figure 4.—Fecundity estimates for swordfish from Hawaiian waters.

should be pointed out, however, that while nonrandom distribution of ova diameters within an ovary may contribute to errors in fecundity estimates, other factors are equally important in making the current methods of measuring fecundity difficult. Other factors include inaccurate estimates of the true ovary weight due to varying amounts of connective tissue left on the ovary surface, and more important, the varying amount of excess fluids (primarily the preservative) removed from the ovary during the "draining" period. Possibly the most important error factor may be related to the point in maturation when the fecundity estimates are made. In species with multimodal frequency distributions of ova diameters (Yuen, 1955; Otsu and Uchida, 1959), the most advanced modal size group has fewer ova than the modal groups to the left (smaller ova). This suggests that resorption of some ova is taking place. Thus, the final number of ova extruded during spawning is less than the number with which the modal group started when the mode first differentiated from the primordial ova stock.

Fecundity estimates of the eight swordfish with early ripe or ripe ova are shown in Figure 4. As indicated in an earlier section, fecundity estimates from three of the fish were based on preserved ovary weights which were estimated from fresh-preserved ovary weight relationship. In Figure 4 two of the eight points appear to be displaced a considerable distance from the general curvilinear relationship of increasing fecundity with increasing fish size. Sample BB-5 with an estimated 914 million ova is considerably higher than the general trend, while sample BB-1 with 2.2 million ova is on the lower side.

From our limited fecundity data, and considering the error factors described above, we estimate the fecundity of swordfish to range from 3.0 million ova for a fish weighing 80 kg to 6.2 million ova for a fish weighing 200 kg. Yabe et al. (1959) estimated the fecundity of a 186 cm (orbit to fork) swordfish to be between 3 and 4 million ripe ova.

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APPENDIX: Table 1.—Frequency distribution of ripe ova diameters from selected parts of a swordfish ovary (sample BB-3).

Ocular micrometer units	Milli- meters	Subsamples[1] RAC	RAM	RAO	RMC	RMM	RMO	RPC	RPM	RPO	LAC	LAM	LAO	LMC	LMM	LMO	LPC	LPM	LPO
87	1.7835	1	—	1	2	—	—	2	—	1	—	—	—	—	—	—	—	—	—
86	1.7630	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
85	1.7425	—	2	—	—	—	—	1	—	—	—	—	1	—	—	—	1	—	—
84	1.7220	1	—	—	—	—	2	1	1	2	—	1	—	—	—	1	—	2	—
83	1.7015	—	—	1	1	—	2	3	2	5	1	1	1	—	1	—	—	1	1
82	1.6810	—	3	1	—	2	4	3	2	4	1	1	4	1	—	2	—	1	1
81	1.6605	2	2	1	3	2	3	2	4	2	3	3	2	3	2	1	1	1	2
80	1.6400	5	2	4	4	4	4	3	7	10	4	3	6	5	2	2	4	1	1
79	1.6195	4	4	6	3	4	3	2	2	7	—	5	2	2	4	4	3	8	3
78	1.5990	4	6	6	6	3	7	10	11	9	7	5	8	5	2	3	5	5	3
77	1.5785	4	6	9	1	8	2	13	14	12	5	8	8	10	4	8	11	9	11
76	1.5580	10	14	8	8	5	12	9	3	14	7	9	10	7	10	11	3	5	10
75	1.5375	4	11	8	12	8	10	5	13	7	11	6	3	10	5	12	9	13	12
74	1.5170	7	11	11	7	5	4	7	11	8	7	17	12	17	10	12	7	9	8
73	1.4965	11	13	7	10	12	7	10	13	20	16	20	15	13	11	13	14	14	11
72	1.4760	21	13	11	11	13	10	10	10	15	11	14	17	10	18	19	13	14	11
71	1.4555	18	16	6	4	7	8	9	6	7	16	16	18	11	9	11	14	18	16
70	1.4350	14	15	10	8	15	10	7	11	12	12	15	16	16	13	13	21	11	18
69	1.4145	10	5	11	6	7	7	8	8	10	7	11	4	9	14	8	13	6	12
68	1.3940	20	11	9	15	16	7	12	11	12	17	8	10	20	12	10	16	12	10
67	1.3735	14	11	19	11	8	13	11	8	14	12	5	12	12	10	16	10	11	21
66	1.3530	6	9	10	13	11	9	17	8	3	10	8	4	8	9	5	10	8	13
65	1.3325	7	6	12	11	10	16	6	7	3	5	7	12	9	8	6	5	5	6
64	1.3120	4	8	5	7	2	5	7	9	4	8	2	6	3	12	11	9	9	6
63	1.2915	10	4	8	13	6	9	4	9	4	6	7	6	4	9	5	7	5	6
62	1.2710	3	9	5	4	6	5	6	7	1	12	8	5	4	10	4	8	7	4
61	1.2505	3	3	3	3	6	8	9	2	2	4	5	4	4	3	2	4	9	2
60	1.2300	5	4	1	5	7	4	6	4	3	5	4	2	9	6	6	1	1	5
59	1.2095	2	3	2	4	5	3	2	5	2	1	—	1	1	1	3	2	1	1
58	1.1890	2	—	4	5	6	3	3	4	—	3	—	6	3	1	3	4	6	4
57	1.1685	1	2	6	6	5	9	2	2	1	2	2	—	—	4	2	1	1	1
56	1.1480	1	1	2	2	3	—	—	2	1	1	2	—	—	1	—	1	1	—
55	1.1275	2	1	1	2	6	4	1	1	1	1	—	1	2	2	2	—	1	—
54	1.1070	—	1	4	5	3	—	1	—	1	1	1	3	1	1	2	1	—	—
53	1.0865	2	—	2	2	1	1	1	1	—	1	1	—	—	1	1	1	1	—
52	1.0660	1	1	3	3	1	3	3	—	1	—	—	—	—	1	—	1	1	—
51	1.0455	—	1	—	1	—	2	1	—	2	2	2	1	—	1	1	—	—	—
50	1.0250	—	—	2	—	—	—	1	—	—	1	2	—	—	1	1	—	—	—
49	1.0045	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
48	.9840	1	—	—	1	1	—	—	1	—	—	—	—	1	2	—	—	—	—
47	.9635	—	—	—	—	1	1	—	1	—	—	—	—	—	—	—	—	1	—
46	.9430	—	—	1	1	1	2	—	—	—	—	—	—	—	—	—	—	2	—
45	.9225	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—
44	.9020	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[1]
RAC - Right anterior center
RAM - Right anterior mid-layer
RAO - Right anterior outer layer
RMC - Right middle region center
RMM - Right middle region mid-layer
RMO - Right middle region outer layer
RPC - Right posterior region center
RPM - Right posterior region mid-layer
RPO - Right posterior region outer layer
LAC - Left anterior center
LAM - Left anterior mid-layer
LAO - Left anterior outer layer
LMC - Left middle region center
LMM - Left middle region mid-layer
LMO - Left middle region outer layer
LPC - Left posterior region center
LPM - Left posterior region mid-layer
LPO - Left posterior region outer layer

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Synopsis of Biological Data on Striped Marlin, *Tetrapturus audax* (Philippi), 1887

SHOJI UEYANAGI[1] and PAUL G. WARES[2]

IDENTITY

1.1 Nomenclature

1.11 Valid Name

Tetrapturus audax (Philippi), 1887 is the name adopted by the most recent review of the family (Nakamura, Iwai, and Matsubara, 1968). The original combination was *Histiophorus audax* Philippi, 1887. Anal. Univ. Chile 71:34-39.

1.12 Objective synonymy

All synonyms are assumed to be subjective without consulting original papers and are listed under section 1.21.

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Chordata
  Subphylum Vertebrata
    Superclass Gnathostomata
      Class Osteichthyes
        Subclass Actinopterygii
          Order Perciformes
            Suborder Xiphioidei
              Family Istiophoridae

Generic

Genus *Tetrapturus* Rafinesque, 1810.

Caratteri di alcuni nuovi generi e nuove specie di animali [principalmente di pesci] e piante della Sicilia, con varie osservazioni sopra i medisimi. Palermo, 105 p.

Type-species *Tetrapturus belone* Rafinesque, 1810.

Robins and de Sylva (1960, 1963) placed the striped marlin in *Tetrapturus*, following the works of hierarchical classification of the family by Hirasaka and Nakamura (1947) and Nakamura (1949). This placement of *audax* in *Tetrapturus* is supported by Ueyanagi (1963b), Howard and Ueyanagi (1965), and Nakamura et al. (1968).

We follow the generic concept of Nakamura et al. (1968), who described the genus as follows:

> The height of the dorsal fin is greater than the body depth. The ventral fin rays are rather long, the fin membrane not well developed. The body is compressed (flat) and except for the striped marlin (Makajiki) and the white marlin (Nishimakajiki), extends in a straight line from the pre-occular area to the base of the dorsal fin. The cranium is long and narrow. The neural and haemal spines of the central vertebrae form a parallelogram. There are 24 vertebrae (12 + 12 = 24). The lateral appophysis[3] is not well developed.

These authors include the following species in the genus: *T. angustirostris* Tanaka, 1914; *T. belone* Rafinesque, 1810; *T. pfluegeri* Robins and de Sylva, 1963; *T. albidus* Poey, 1861; *T. audax* (Philippi, 1887).

Specific

Identity of type specimen:

Species *T. audax* (Philippi, 1887).

Type specimen: Apparently one of the two deposited in the Museo Nacional de Historia Natural, Santiago, Chile by Rudolfo A. Philippi.

Type Locality: Iquique, Chile.

Diagnosis: Ventral fins and two caudal keels are present; snout cross section is nearly circular; first dorsal fin anteriorly is about same height as body depth or greater[4] and is not saillike but slopes abruptly posteriorly, the middle rays being much shorter than the anterior; snout is fairly long; vent is located very close in front of first anal fin; pectoral fins are fairly broad and long and fold against body; and the tips of pectorals, first dorsal, and first anal fins are pointed.

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[3] See Ueyanagi and Watanabe (1965) for usage of this term.

[4] Due to allometric growth of the dorsal fin relative to body depth the fin height may be less than body depth in fish larger than 360 cm FL (Royce, 1957).

Subjective synonymy:

Histiophorus audax	Philippi, 1887
Istiophorus audax	Delfin, 1901
Tetrapterus mitsukurii	Jordan and Snyder, 1901
Tetrapturus ectenes	Jordan and Evermann, 1926
Makaira audax	Jordan and Evermann, 1926
Makaira grammatica	Jordan and Evermann, 1926
Makaira holei	Jordan and Evermann, 1926
Makaira mitsukurii	Jordan and Evermann, 1926
Makaira zelandica	Jordan and Evermann, 1926
Marlina mitsukurii	Grey, 1928
Marlina zelandica	Whitley, 1937
Kajikia mitsukurii	Hirasaka and Nakamura, 1947
Kajikia formosana	Hiraska and Nakamura, 1947
Tetrapturus tenuirostratus	Deraniyagala, 1951
Tetrapturus acutirostratus	Deraniyagala, 1952
Makaira formosana	Matsubara, 1955
Tetrapturus brevirostris	Munro, 1955
Marlina audax	Smith, 1956a, b
Marlina jauffreti	Smith, 1956b
Tetrapturus audax	Robins and de Sylva, 1960
Makaira jauffreti	Jones and Silas, 1964

Artificial key to genus (Nakamura et al., 1968):

A. Anterior fin rays of first dorsal fin fairly high, posterior rays about same height; vent situated decidedly anterior to origin of the first anal fin; second anal fin anterior to second dorsal fin.

B. Pectoral fin narrow and short

C. Snout very short. . . Shortbill spearfish (Furaikajiki) *T. angustirostris* Tanaka.

CC. Snout fairly long . . . . Mediterranean spearfish (Chichukaifurai). *T. belone* Rafinesque.

BB. Pectoral fin wide and long . . . . .Longbill spearfish (Kuchinagufurai) *T. pfluegeri* Robins and de Sylva.

AA. Height of anterior portion of first dorsal fin about same as the body depth but gradually decreasing in height posteriorly; vent directly anterior to the origin of the first anal fin; second dorsal fin and second anal fin in parallel positions.

D. Pectoral fin wide and its tip rounded. The tip of the first dorsal fin and first anal fin rounded . . . . White marlin (Nishimakajiki) *T. albidus* Poey.

DD. Pectoral fin narrow, and its tip pointed; the tips of the first dorsal fin and first anal fin pointed . . . . Striped marlin (Makajiki) *T. audax* (Philippi).

1.22 Taxonomic status

The species is established on the basis of morphology without breeding data.

The species may be polytypic (see 1.31 below).

1.23 Subspecies

No subspecies are recognized.

1.24 Standard common names and vernacular names

Country	*Standard common name*	*Vernacular name(s)*
Sri Lanka		Seraman Koppara
Chile		Pez aguja
China		Chi zuo fo yii
Japan	Makajiki	Maka, Kajiki, Kajikimaguro, Nairagi, Nairage, Nairanbo
Kenya		Nduaro
Mexico	Marliń rayado	Marliń, agujon, pez puereo
New Zealand	Striped marlin	New Zealand marlin
Philippines		Spearfish
Russia		Polosatii marlin
Taiwan	Hung ju chi yii	Hung ju ting pan
United States	Striped marlin	Pacific striped marlin, barred marlin, Pacific marlin, striped swordfish, spearfish, spikefish
Vietnam		Ca co Mitsukurii

1.3 Morphology

1.31 External morphology (for description of spawn, larvae, and adolescents, see 3.17, 3.22, 3.23).

Generalized: Gregory and Conrad (1939) provide a scale diagram of the striped marlin outline based on modal body proportions of 30 specimens from New Zealand and Australia using standard length as the basic body measurement. Thirty-eight measurements were made on each specimen and are published in absolute and as percentage of standard length along with total body weight.

Nakamura et al. (1968) provide the following description:

> *External Characters.* The first dorsal fin has 37-42 fin rays. The second dorsal fin has 6 soft rays. The first anal fin has 13-18 fin rays. The second anal fin has 5-6 soft rays. The pectoral fin has 18-22 soft rays. The ventral fin has one spine and 2 soft rays. The

> body is elongated (the body length is about 5.9-7.3 times the body depth) and is rather thick. The snout is long (the head length is about 0.88-0.99 times the length of the maxillary), and its cross-section is almost round. The body is densely covered with scales; the tips of the scales are pointed. Scales from specimens less than 1 meter in length do not have this species characteristic. There are small file-shaped teeth on both jaws and on the palate. The lateral lines on the sides curve over the pectoral fin and then continue in a straight line to the area of the caudal fin. The head is large (the body length is 3.6-3.8 times the length of the head). The eyes are moderately large. There is a relatively conspicuous crest on the outer edge of the head between the pre-occular region and the origin of the first dorsal fin. There are 2 scutes on each side of the tail near the caudal peduncle; the tail is strong and deeply forked. The pectoral fin, has a pointed tip and is located rather low on the body; it is shorter than the head (the head length is about 1.14-1.99 times the length of the pectoral fin). The first dorsal fin begins above the posterior end of the pre-opercle bone; its first few rays are larger than the body depth, but as it progresses towards the back, it gradually becomes shorter, ending just in front of the origin of the second dorsal fin. The tip of the first anal fin is pointed, large and sickle-shaped. The second dorsal fin and the second anal fin are about the same size and shape. The latter is located a little further forward on the body than the former. In spite of the fact that the ventral fin is longer than the pectoral fin in smaller specimens, the opposite is true for larger specimens. The fin membrane of the first dorsal fin is dark blue. The back of the body is dark blue with splotches of black on it; towards the ventral side of the body, 10 or more rows of cobalt-colored stripes are clearly visible. The other fins are blackish brown, or sometimes a dark blue. The bases of the first and second anal fins are silvery-white.

Morrow (1952a) published morphometric data on 49 specimens from New Zealand and later (Morrow, 1957) published extensive morphometric data and anal ray counts on 39 fish from Peru. These data include standard length as the basic body length measurement. Ueyanagi (1957b) presented morphometric data on young specimens, 80- to 180-cm eye-fork length, from the western North Pacific. Royce (1957) reported extensive morphometric data of 75 specimens from the central Pacific using fork length as the basic measurement but also giving standard length and eye-fork lengths for some specimens. He also published more limited data on 30 specimens measured by the Hawaii Division of Fish and Game. Kamimura and Honma (1958) published morphometric data on five characters using eye-fork length as the basic body measure for 56 fish south of the equator and 124 fish north of the equator in the western Pacific. Williams (1967) presented dorsal and anal fin ray counts of 13 specimens from East Africa. Merrett (1971) gives fin measurements on about 23 other specimens.

Counts have been given by several authors and are shown in Table 1.

Georgraphic variation: Geographic variation appears to be considerable. Morrow (1957) concluded that striped marlin from Peru and northern New Zealand represented separate and distinct populations based on significant differences in 11 morphometric and meristic characters as follows: average absolute lengths of pelvic fins, counts of spines and rays in the first anal fin, and the regressions of the following measurements on standard length: greatest body depth, length of base of second dorsal fin, length of base of first anal fin, width of base of pectoral fin, snout tip to origin of first dorsal fin, snout tip to origin of second dorsal fin, snout tip to origin of first anal fin, snout tip to posterior edge of operculum, snout tip to posterior end of maxillary. By a character index (CI) in which

$$\text{CI} = \frac{\text{pelvic length}}{10} - \frac{100}{\text{SL}} \text{ (Depth + Length}$$

of anal base + Width of pectoral base), Morrow could separate correctly about 72% of the 69 specimens from which the index was derived. The New Zealand specimens tended to have character indices of considerably lower numerical value than the Peru specimens.

In the western Pacific (west of long. 170°W) Kamimura and Honma (1958) found a remarkable difference in the lengths of the pectoral fins between northern (lat. 30°-35°N) and southern (lat. 18°-25°S) striped marlin. Covariance analysis of regression of pectoral fin on eye-fork length showed no significant difference in slope of regression but a highly significant (0.01) difference in adjusted means. Also significant differences (0.05) were found for both regression coefficients and adjusted means for regressions of eye-to insertion of second dorsal on eye-fork length. From these differences these authors concluded northern and southern populations in the western Pacific were extremely separated. In intermediate waters of the northern hemisphere (lat. 5°-25°N) all but three fish had pectoral lengths clustered about the regression line for the northern population. The pectoral lengths of the other three fish, which were taken from lat. 5° to 15°N, were close to the regression line for the southern population and were presumed to have strayed from that population.

Honma and Kamimura (1958) supported the hypothesis of separate north and south populations in the western Pacific with the following observations:

a) a zone of low hook-rate along the equator separates the populations;
b) the main spawning grounds are widely separated and spawning seasons are a half-year apart;
c) the maximum size attained is much larger in the southern population;
d) adaptations of the two populations to environmental circumstances do not coincide in details, differing with growth stages.

Howard and Ueyanagi (1965) extended the

Area and author	First dorsal fin	dorsal fin	First anal fin	anal fin	Pelvic fins	Pectoral fins
Chile Philippi, 1887	38	5	12	5	1	
Western Pacific Nakamura, 1938, 1949	37-43 (III+12−15+XXII−XXV)	6	14-15 (II+12−13[1])	6	1+2	
Western Pacific Ueyanagi, 1959	37-44					
New Zealand Morrow, 1957			12-16			
Peru Morrow, 1957			14-17			
East Africa Williams, 1967	35-41	5-7	11-15	5-6		
Peru Morrow (unpubl.) (after Williams, 1967)	37-44	5-7	14-17	5-7		
East Africa Morrow (unpubl.) (after Williams, 1967)	36-41	5-7	11-15	5-6		
East Africa Merrett, 1971	38-42	5-7	13-16	5-6		19-23
Eastern North Pacific Wares and Sakagawa, 1974		5-7		5-7		

[1] The figure of 25 which appears here in the translation of the 1949 paper is evidently a misprint.

hypothesis by including eastern Pacific fish in the southern population and demonstrating that growth of the pectoral fin is allometric with an inflection at about 185-cm eye-fork length. They pointed out that mixing of the two populations occurs in the tropics and suggested that Mexican fish belong principally to the southern-eastern group and that southern California fish are derived from both groups but dominated by the northern.

Merrett (1971) found striped marlin of the tropical western Indian Ocean to have relatively long pectoral fins indicating a closer relation to the southern-eastern population than to the northern.

There has been little mention in the literature of geographical variation in color pattern, but the striking almost zebralike bars on the freshly caught New Zealand specimen in the photo published by Gregory and Conrad (1939) appears more pronounced than in fish from other regions.

To date, the knowledge of subpopulations, if they truly exist, is insufficient for morphological definition.

The morphological changes of larvae and adolescent phases are of course remarkable. See 3.22 and 3.23.

Morrow (1952a) found significant ($P < 0.001$) negative allometry in the dorsal and ventral lobes of the caudal fin and a slight but not statistically significant ($P = 0.065$) negative allometry in the length of the pectoral fin of 49 adult fish from Cape Brett, New Zealand. The pelvic fins show extreme negative allometry appearing to cease growth after reaching a certain size (Morrow, 1957; Royce, 1957). Negative allometry was found in Peruvian specimens for body depth and snout tip to origin of first anal fin (Morrow, 1957). Ueyanagi (1957b) found extreme negative and positive allometry, respectively, in central dorsal rays relative to body depth and pectoral length relative to body depth in young specimens (85-175 cm) which proved the synonymy of *Kajikia formosana* and *T. audax.* Royce (1957) also found similar allometry.

Ontogenetic change in body form is shown in Figure 1. The morphological change of the snout (its growth relative to the body length) from the postlarval to adult stage of striped marlin is relatively small in comparison with those of other istiophorid species. However, the change of the dorsal fin shape during growth is remarkable in this species (Ueyanagi, 1963b).

In relation to functional morphology, Fierstine (1968) found an average aspect ratio (span/surface area of one side of fin) of 9.0 for the caudal fin of three striped marlin from the eastern Pacific. This high ratio, indicating relative efficency as a hydrofoil, was greater than that for seven other scombroid species but less than that for the sailfish, *Istiophorus platypterus*, and the white marlin, *T. albidus* (10.0 and 10.3, respectively).

Published weight-length regression constants are summarized in Table 2.

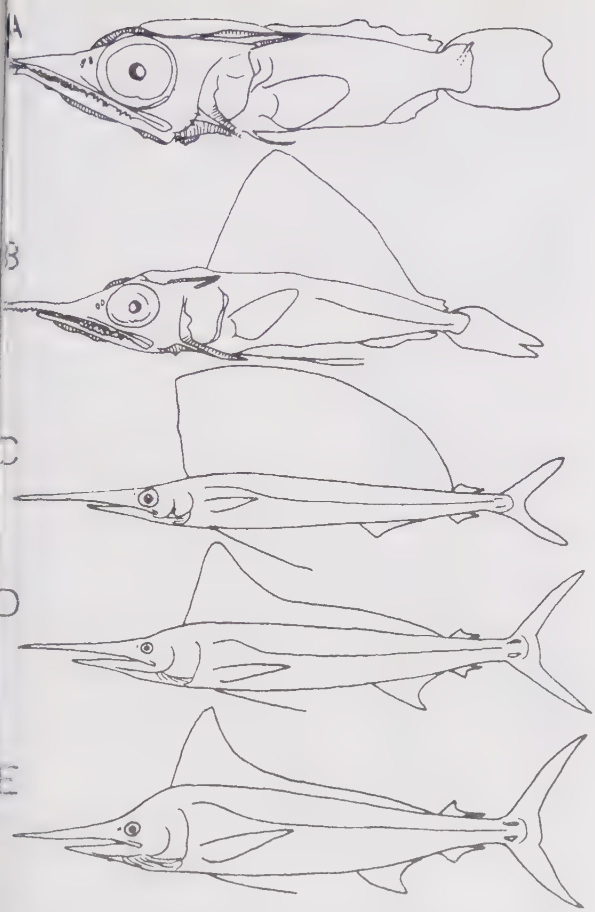


Figure 1.—Ontogenetic change in body form of striped marlin. A. 7.9 mm SL, B. 21.2 mm SL, C. 121.5 mm body length, D. 1,050 mm body length, E. 1,882 mm body length. (From Nakamura, 1968.)

1.32 Cytomorphology

No data available.

1.33 Protein specificity

No data available.

2 DISTRIBUTION

2.1 Total Area

In the eidogical classification of Parin (1968) the triped marlin is holoepipelagic, i.e., it inhabits the sothermic surface pelagic layer of the ocean at all tages of its life cycle. Such species are chiefly limited in distribution to the tropics, where a permanent thermocline exists, but penetrate higher latitudes in the warm season. Atypical of the distribution of most scombroids, the striped marlin seems to prefer the more temperate waters. In the Pacific the distribution resembles that of the albacore, *Thunnus alalunga*, and bluefin tuna, *T. thynnus*, in contrast to that of the other billfishes and tunas (Howard and Ueyanagi, 1965; Parin, 1968), however, in the Indian Ocean the striped marlin distribution is centered in warmer waters.

Striped marlin occur throughout the warmer waters of the Indian and Pacific oceans. The species ranges eastward to the coast of the American continents and westward to the African coast. Off South Africa they are found a slight distance into Atlantic waters (Talbot and Penrith, 1962). Extreme poleward distribution has been recorded to lat. 40°-45° in both hemispheres. In the north this occurs in the Kuroshio extension, primarily between long. 165°E and 180°, but also at long. 150°W (Fisheries Agency of Japan, Research Division, 1969-71). In the southern hemisphere this occurs in the Agulhas Current (Talbot and Penrith, 1962; Fisheries Agency of Japan, Research Division, 1969-72) and also rarely at long. 105°E (Fisheries Agency of Japan, Research Division, 1969), which appears to be West Wind Drift water. On the eastern perimeter of the Pacific, Point Conception (lat. 35°N) and Chañaral, Chile (lat. 29°S) appear to be the northern and southern limits of distribution.

The broad geographical distribution of this species makes it difficult to generalize on the physical and biological characteristics of the areas inhabited. Temperature, however, is one parameter which has been considered to influence total distribution. The 20° and 25°C isotherms tend generally to bound the total distribution at least in the western Pacific (Howard and Ueyanagi, 1965).

2.2 Differential Distribution

2.21 Spawn, larvae, and juveniles

Although information is lacking on the distribution of eggs, there are several reports (Ueyanagi, 1959, 1964; Jones and Kumaran, 1964; Nishikawa and Ueyanagi, 1969) pertaining to the distribution of larvae.

In the Pacific, larvae have been observed in the northwestern Pacific (west of long. 180°) between lat. 10° and 30°N; and in the South Pacific (west of long. 130°W) between lat. 10° and 30°S. The larvae are most abundant in early summer, with the peak occurrence in the northwestern Pacific during May-June, and in the South Pacific in November-December. The seasonal occurrence of mature females coincides with that of the larvae (Ueyanagi, 1964). While the distribution of larvae is not known for the

Table 2.—Weight-length constants for *Tetrapturus audax* ($\log W = \log a + b \log L$).

Location	Weight	Units of weight	Length	Units of length	Number	Approximate length range of specimens	a	b	s	Source
New Zealand and Australia	Whole	lb	FL[1]	cm	27	265-310	−6.515	3.624	0.045	Gregory and Conrad, 1939 (after Royce, 1957)
New Zealand	Whole	lb	FL[1]	cm	48	218-310	−5.024	3.011	0.056	Morrow, 1952a (after Royce, 1957)
Central Pacific	Whole	lb	FL	cm	13	142-304	−6.648	3.691	0.502	Royce, 1957
Hawaii	Whole[2]	lb	FL[3]	cm	30	166-253	−6.110	3.446	0.048	Hawaii Division of Fish and Game (after Royce, 1957)
East Africa	Whole	lb	FL	cm	98	170-270	−4.629	2.844	?	Williams, 1967
Fiji area	Gilled and gutted	kan[4]	Eye-fork[2]	cm	562	160-260	−6.737	3.504	?	Koga, 1967
Equatorial west Indian Ocean	Whole	lb	Eye-fork	cm	156	120-196	−4.782	[5]3.062	?	Merrett, 1968c
Eastern Pacific	Whole	kg	Eye-fork	cm	51	108-211	−5.255	3.089	?	Kume and Joseph, 1969b
Eastern Pacific	Whole	lb	Eye-fork	cm	1,982	110-215	−4.816	3.072		Wares and Sakagawa, 1974
Eastern Pacific	Whole	kg	Eye-fork	cm	1,982	110-215	−5.157	3.071		Wares and Sakagawa, 1974
Eastern Pacific	Whole	lb	FL	cm	535	153-271	−5.007	2.986		Wares and Sakagawa, 1974
Eastern Pacific	Whole	kg	FL	cm	535	153-271	−5.340	2.982		Wares and Sakagawa, 1974

[1] The original measurement was SL which apparently Royce converted to FL on the basis of regression for nine Hawaiian specimens and mislabeled "*total*" length in caption to Appendix Table 3-A.

[2] Presumed.

[3] The original measurement was naris to fork which Royce converted to FL on the basis of regression for 21 Hawaiian specimens.

[4] 1 kan = 3.75 kg = 8.287 lb.

[5] ±0.197.

stern Pacific (east of long. 120°W), mature fish are ported to occur there between lat. 5° and 20°N, rgely in May-June (Kume and Joseph, 1969b).

In the Indian Ocean, larvae have been reported to ccur in the Banda and Timor seas during January to ebruary (Ueyanagi, 1959), and in the western Indian cean during December to January between lat. 10°S nd 18°S and in the eastern Indian Ocean during Oc- ber to November between lat. 6°N and 6°S (Jones nd Kumaran, 1964). Mature females are reported to ccur in March-May in the Bay of Bengal although rval occurrence is not yet known there (Ueyanagi, 964).

The lower temperature limit in the distribution of rvae is approximately 24°C both in the Indian and acific oceans. However, the distributions differ in hat in the Pacific the larvae are scarcely found in quatorial waters. It is noted that striped marlin larae are not likely to appear in the Kuroshio area, hile sailfish larvae occur there exclusively Ueyanagi, 1959).

Information is very sparse on the distribution of the uveniles. Nakamura (1968) reported on two juveniles body length, 12.15 and 14.5 cm) found in stomachs of yellowfin tuna, *Thunnas albacares*, and a dolphin, *Coryphaena hippurus*, taken by longline. One juvenile was found on 13 January 1955 at lat. 23°52′S, long. 75°49′W and the other on 21 December 1964 at lat. 7°57′S, long. 67°29′E. These two occurrences coincide with larval distributions in the South Pacific and ndian Ocean, respectively.

2.22 Adults

Major areas of high abundance are the western Arabian Sea, the central North Pacific (lat. 15°-30°N) and the eastern Pacific as shown in Figure 2. This figure shows distributions based on highest quarter-year hook rates by 5° squares for the years 1967-69 (Fisheries Agency of Japan, Research Division, 1969-72). Lesser areas of abundance occur off South Africa, northern Madagascar, northern Sumatra, Sri Lanka, eastern and western Australia, central Pacific coast of Japan, and the south central Pacific.

The high density in the Arabian Sea appears to be seasonal, occurring in the second quarter of the year. However, fishing effort in other seasons has been very slight. Off East Africa (lat. 0°-12°S) where striped marlin are the most abundant marlin, the works of Merrett (1968a, b) showed highest hook rates occurred between lat. 2° and 4°S. The hook rate was six times higher in the northeast monsoon (Nov.-Mar.) than in the southeast monsoon (Apr.-Oct.).

The season of high abundance off western and eastern Australia is the fourth quarter (Fisheries Agency of Japan, Research Division, 1969-72). Koga (1967) states, however, that good catches occur in winter off western Australia. In the South Pacific, Koga states that it is a remarkable feature that the main fishing areas, which show good catches from August to December, show very poor catches from January to July.

In the northwestern Pacific, striped marlin are abundant in Formosan waters, both in the Kuroshio and in the South China Sea, during the whole northeast monsoon season with a peak in the middle of that season. Later in the spring, they move north into the waters of Japan where they appear at about the same time as the albacore do (Nakamura, 1949).

In the Hawaiian area, striped marlin occur from fall through spring with the seasonal distribution being

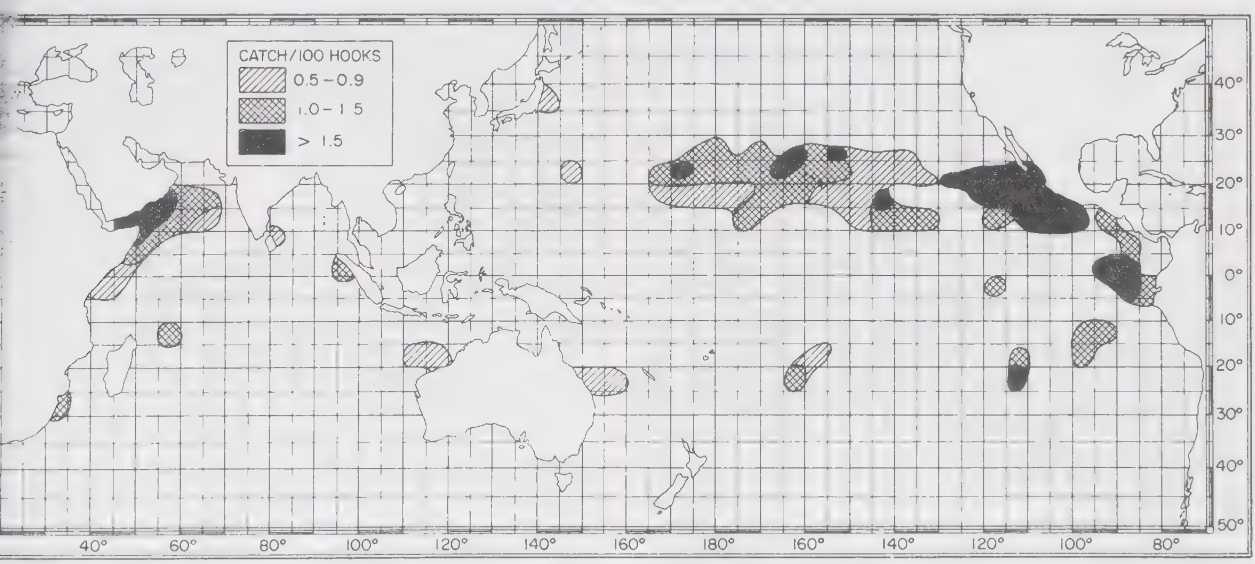


Figure 2.—Areas of high apparent abundance of striped marlin, 1967-69. (After Fisheries Agency of Japan, Research Division, 1969-72.)

complimentary to that of the blue marlin, *Makaira nigricans*, which occurs primarily in the summer (Strasburg, 1970).

In the eastern Pacific, striped marlin are present throughout the year from lat. 30°N to 30°S. High abundance is maintained throughout the year in the areas of the Revilla Gigedo Islands, Baja California, Ecuador, the Galapagos Islands, and in the high-sea area bounded by long. 90°-110°W and lat. 10°-30°S (Kume and Joseph, 1969b). Seasonal changes in apparent density are marked. The concentration between Baja California and the Revilla Gigedo Islands, which is restricted to a narrow band in the first quarter, expands southeast along the coast and seaward to long. 115°W during the second quarter, and then north to lat. 28°N, south to lat. 3°N and seaward to long. 125°W during the third quarter. During the fourth quarter the southern extension expands further to long. 130°W. Another seasonal concentration develops in the second and third quarters in the offshore area between long. 100° and 115°W centered at about lat. 8°-13°N. The area of high density around the Galapagos Islands extends eastward to the coast of Ecuador in the third and fourth quarters and then recedes again in the first.

The sport fisheries for striped marlin off Mexico and southern California are seasonal. In southern California it is highly seasonal with almost all fish being taken between August and October. In Mexico some fish may be taken year round, but the best fishing occurs from December through March at Mazatlán and April through August near the tip of Baja California (Eldridge and Wares, 1974).

In addition to differential distribution in density, there is also some differential distribution in size. In the eastern Pacific, fish on the southern spawning grounds are larger than those on the northern. The length frequency of the southern group has a single mode at 180-200 cm whereas that of the northern group has two modes, one at 140 cm and one at 180 cm (Kume and Joseph, 1969b). In the western Pacific latitudinal stratification occurs. Honma and Kamimura (1958) show small marlin occurring in equatorial waters; these small fish are absent in the region of lat. 5°-16°S. In mid-latitudes (15°-30°S) of the central South Pacific longitudinal stratification is apparent; larger fish (> 180 cm) occur in the western Pacific (Koga, 1967). There may also be some vertical stratification. Furukawa, Koto, and Kodama (1958) found harpooned fish to be larger than longline-caught fish in the East China Sea. The harpooned fish were also fatter at a given length.

Off Formosa the smaller fish, which were long thought to be the separate species *Kajikia formosana*, occur with the shortbill spearfish, *Tetrapturus angustirostris*, offshore from the center of the Kuroshio, while the larger fish occur inshore (Nakamura, 1949).

2.3 Determinants of Distribution Changes

Probably behavioristic factors related to feeding and reproduction are the primary determinants of changes in distribution. These in turn are affected by the seasonal cycle of warming of the surface waters, development of thermoclines and currents, and seasonal cycles in abundance of food organisms. The subject of the factors and relationships causing concentration of striped marlin has not received much discussion in the literature.

Nishimura and Abe (1971) have found a correlation between the position of the Kuroshio as indicated by the latitude at which the current crosses 139°30′E, and the catch made off Izu.

Kume and Joseph (1969b) noted that the appearance of the area of high hook rate centered at lat. 8°-13°N from long. 100° to 115°W is associated with the strong development of the Equatorial Countercurrent. They noted further that a diagonal band of high abundance extending from lat. 5°S, long. 120°W to lat. 8°S, long. 95°W was in the general region of the eastern extension of the South Equatorial Countercurrent.

In the area west of Australia, both the striped marlin and southern bluefin tuna grounds are centered at the boundary of currents which run along long. 115° E meridian in winter (Koga, 1967).

Manning (1957) states that off Chile, striped marlin are found in the green water that is normally found from shore to 10 to 25 miles offshore. Their occurrence in these waters was in common with bonito, sardines, and anchovies and in contrast to swordfish which occurred farther offshore in the blue and white waters.

Furukawa et al. (1958) show the fishing ground in the western Pacific associated with the surfacing of the 20°C isotherm over the edge of the continental shelf.

Nakamura (1938) states that surfacing of fish is associated with high waves generated by opposing wind and current as in the case of the Kuroshio and the northeast monsoon.

2.4 Hybridization

No record.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Striped marlin are heterosexual with no reported intersexuality or hermaphroditism.

Sexual disorphism has not been reported in this species and the sexes are indistinguishable externally. Nakamura (1949) mentioned the sexual difference in body size is not great in the genus *Tetrapturus* in contrast to the case in *Makaira*. Differences in greatest ze or modal size between the sexes are small. eyanagi (1953) found, in the northwestern Pacific, hat the modal size of males is about 10 cm smaller han that of females. Koga (1967) showed a length-requency distribution by sex for 210 fish from the Fiji rea in which the modal lengths for males and females were 195 and 205 cm, respectively. In a sample of 105 triped marlin taken by longline off East Africa, Williams (1967) found males did not exceed 240 cm ork length (equivalent to 182 cm eye-fork length from egression of Merrett, 1971). About 16 females were taken above this length to a size of about 270 cm (205 cm eye-fork length). Merrett (1971), however, found males up to 193 cm eye-fork length off East Africa. Modal size differences between the sexes were not found in Hawaiian fish (Strasburg, 1970) nor in the eastern Pacific (Kume and Joseph, 1969b).

3.12 Maturity

As has been found in other pelagic species such as albacore and dolphin, quantitative measure of maturity for males is difficult. There is only a small increase in testis size during the maturation cycle. Merrett (1971) found little correlation between relative testis size and maturity-stages based on microscopic examinations. In fact, Merrett (1970) suggests that there is continuous availability of spermatozoa in mature males based on differential maturation of the testicular lobules and the possession of a muscular seminal vesicle.

In the female, maturation is synchronous throughout the ovary and seasonal maturation is accompanied by marked increase in relative size of the gonads. Data from Kume and Joseph (1969b) showed a twentyfold increase. Moreover, there is good correlation of relative ovary weight and mean maximum egg diameter (Merrett, 1971; Eldridge and Wares, 1974).

Williams (1967) concluded from longline data in East Africa that first maturity was reached between 180 and 200 cm fork length (50-80 lb) which is equivalent to 141-157 cm eye-fork length (Merrett, 1971). Merrett reported similar results, 140-160 cm or 62-93 pounds. Ueyanagi (1957b) mentioned that 154 cm eye-fork length was the smallest size found in the spawning group of the northwestern Pacific. Kume and Joseph (1969b), using a gonad index, reported that individuals from the eastern Pacific do not regularly enter the spawning group until reaching about 160 cm eye-fork length but found one as small as 148 cm. Other data from the eastern Pacific (Eldridge and Wares, 1974) agree with these conclusions.

Since age at specific size is not known for striped marlin, age at maturity is also unknown. Koga (1967), however, stated "it is likely that growth rate of this species shows different values between the Indian Ocean and the Pacific Ocean and the groups in the Indian Ocean attain maturity earlier than those in the Pacific."

3.13 Mating

Nothing has been published relating to mating habits of this species.

3.14 Fertilization

Fertilization is externally.

3.15 Gonads

Merrett (1970) has described the gonads of billfish in detail. The following description is taken from his work.

> The gonads are paired organs lying in the posterior half of the body cavity, on each side of the stomach and intestine. They are suspended from the lateral edges of the chambered air bladder by mesenteries . . . the gonads are almost bilaterally symmetrical and both terminate at their point of discharge to the exterior in the urino-genital papilla . . . which lies posterior to, and in a common groove with, the anus . . . The urinary and genital systems are closely linked.
>
> The ovaries are elongate sausage-shaped organs, which taper at both ends, and joined only at their posterior ends . . . A strong muscular sheath binds the ovaries to the urino-genital papilla and the basal part of the intestine. They are invested in thick layers of connective tissue which sometimes contain deposits of fat; fat is also occasionally found in the mesovarium. Beneath the connective tissue the ovaries are pale flesh-pink to wine red in colour, depending upon the stage of maturity. Internally, at certain stages, a central lumen runs the length of the ovary . . . the ovaries have been found to be unequal in length . . . either ovary can be the longer of a pair.
>
> . . . Immediately posterior to . . . [the anal papilla] . . . is the urino-genital papilla. In the female this carries only the urinary duct. The point of discharge of the ovaries is situated between the bases of the anal papilla and the urino-genital papilla.

This opening between the anal and urino-genital papillae which is absent in the males should serve as an external characteristic in distinguishing the sexes. But in the experience of the junior author this difference is difficult to observe consistently in this species. It is more obvious in the sailfish.

Nakamura (1949) stated that the fecundity of billfishes ranges from 1 to 1.2 million eggs, depending on fish size and species. Morrow (1964) estimated 2 million eggs for New Zealand marlins. These appear to be low estimates, however. Merrett (1971) reported an estimated fecundity of 12 million for one Indian Ocean specimen of 182 cm eye-fork length, 126 pounds with ovary weight of 1.53 kg, and mean maximum egg diameter of 0.470 mm. Eldridge and Wares (1974) reported fecundity estimates of three eastern Pacific specimens which ranged from 11 to 29 million eggs. These fish ranged in size from 150 to 180 cm eye-fork length but the fecundities showed no relation to size of the fish. Gosline and Brock (1960) estimated 13.8

million eggs were contained in one ovary of a 154-pound striped marlin landed in Honolulu. The other ovary of this fish was immature.

3.16 Spawning

Examination of size-frequency distributions of egg diameters (Eldridge and Wares, 1974) indicates only one spawning per season.

In the western Indian Ocean it appears that the high catch rates during the northeast monsoon period which peak from December to February are associated with a postspawning feeding migration (Williams, 1967; Merrett, 1971). Spawning must occur elsewhere in the Indian Ocean.

From larval occurrence, spawning was suggested to take place in the Banda and Timor seas during January to February (Ueyanagi, 1959). On the basis of larval occurrence, Jones and Kumaran (1964) stated that striped marlin spawn in the western Indian Ocean during December-January between lat. 10° and 18°S and in the eastern Indian Ocean during October-November between lat. 6°N and 10°S. Furthermore mature females are known to occur in March-May in the Bay of Bengal and in October-December in the waters south of the Lesser Sunda Islands (Ueyanagi, 1964).

In the western Pacific, mature females are found from lat. 15° to 30° (north and south) in early summer, from May to June and October to January in the northern and southern hemispheres, respectively. Larvae are also found in these areas (Ueyanagi, 1964). Nakamura (1949) stated that in the Formosa area, spawning is thought to take place mainly in the South China Sea with its peak occurring from April to May. Koga (1967) reported that the spawning areas (lat. 18°-30°S) in the western South Pacific is also the main fishing area and that the period of spawning corresponds to the season of northward migration which occurs from September to November.

In the eastern Pacific, the spawning season also appears to be the early summer in each hemisphere, quarters II and III in the northern and quarters IV and I in the southern. Highest frequencies of spawning fish occur from May to June in the north and November to December in the south (Kume and Joseph, 1969b). Evidence of spawning in the eastern Pacific is based only on relative gonad sizes of females. The northern spawning area appears to be isolated in a narrow band from long. 107° to 114°W extending from about lat. 6° to 19°N (Kume and Joseph, 1969b).

Ovaries of striped marlin caught in the Mexican sport fishery undergo rapid development in June; ripe fish were never observed (Eldridge and Wares, 1974). Japanese fishermen, however, have reported ripe and running ripe striped marlin in the waters around Socorro Island from June to October (J. L. Squire, Jr., Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., pers. commun.).

The southern spawning area appears fairly well confined to lat. 20°-25°S and long. 125°-130°W (Kume and Joseph, 1969b). Highest frequencies of the mature females occur in November and December.

Nakamura (1949) stated that sex ratios approached 1:1 at the peak of the spawning season. However, it was found that males dominate during the spawning season in the northwestern Pacific (Nakamura, Yabuta, and Ueyanagi, 1953). Kuma and Joseph (1969b) also found a high proportion of males in the spawning groups in the eastern Pacific. Male:female ratios ranged from 1.8 to 6.6 in spawning groups, whereas in nonspawning groups they tended to be less than 0.5 and to decrease with increased size of fish.

3.17 Spawn

There is little information pertaining to the eggs of this species. Nakamura (1949) mentioned that the external morphology of the eggs of striped marlin closely resembles that of sailfish eggs which are spherical, transparent, and buoyant, with a single oil globule and with no special structure on the egg membrane. Morrow (1964) reported that the ovarian eggs of striped marlin from New Zealand average about 0.85 mm in diameter. Size of the ovulated eggs of this species is presumed to exceed 1 mm in diameter considering that the mean diameter of eggs for shortbill spearfish is 1.442 mm and for sailfish is 1.304 mm as reported by Merrett (1970).

3.2 Pre-Adult Phase

3.21 Embryonic phase

No information available.

3.22 Larval phase

The postlarval stage of striped marlin is described in detail by Ueyanagi (1959). The study was based on 40 specimens ranging from 2.9 to 21.2 mm in standard length, collected from the northwestern Pacific, South Pacific, and the Indian Ocean. These specimens were captured by surface tows of the larvae net. The morphology of the striped marlin postlarvae is similar to that of other istiophorid species in the development and degeneration of head spination, fin formation, pigmentation, etc. Figure 3 from Ueyanagi (1959, 1963a) represents the postlarval stage of this species from an early stage with short snout to an advanced stage with elongated jaws. The snout begins to lengthen at around 7 mm standard length. Head spination becomes most conspicuous at this size. Fin rays of each fin reach their full complement at around 20 mm standard length. Pigmentation extends almost all over the body surface and on the dorsal fin membrane at this size. The dorsal fin begins to increase its height at around 10 mm and stands very high like a sail in larvae exceeding 20 mm. The key diagnostic character for the striped marlin larvae was reported as

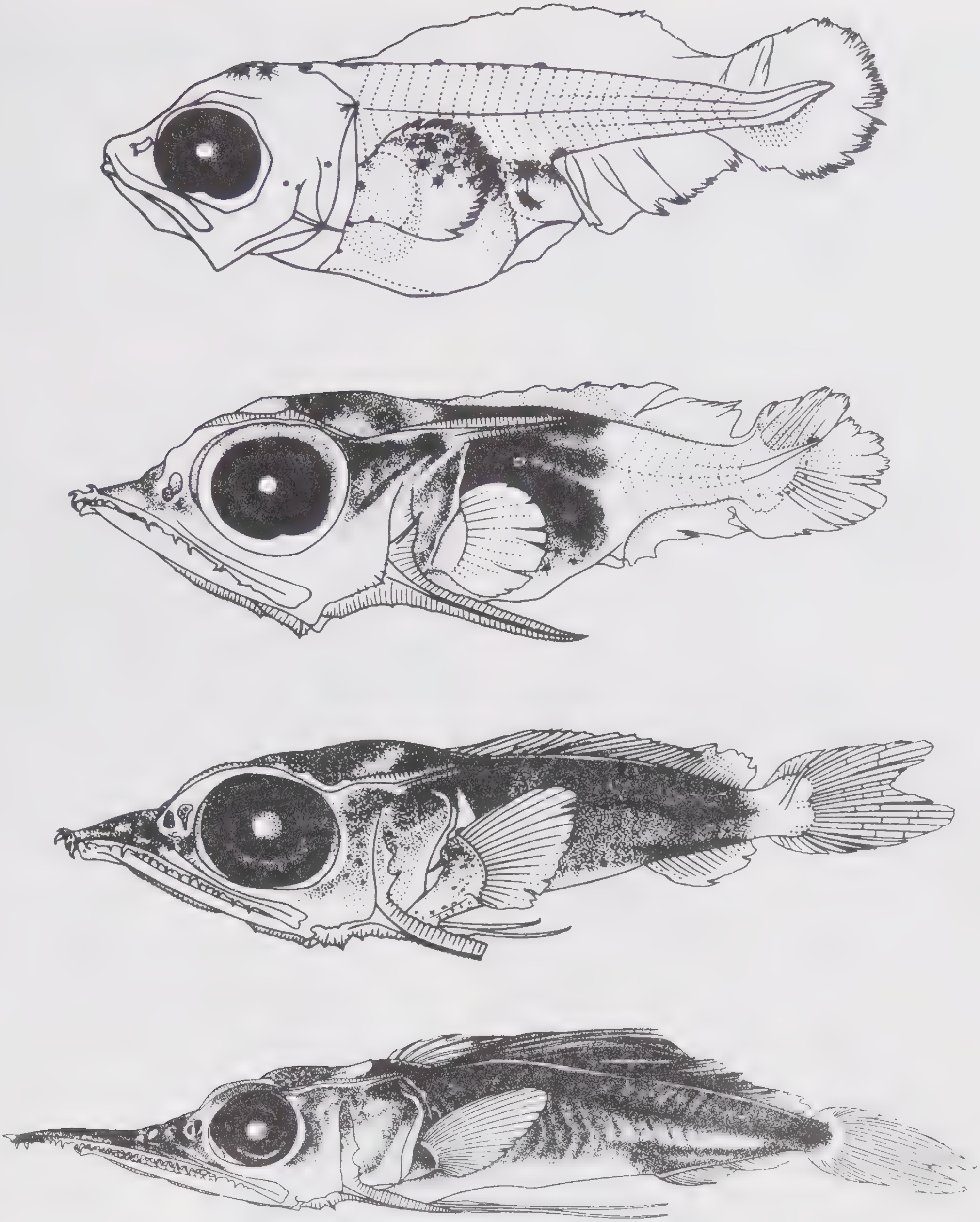


Figure 3.—Larvae of striped marlin. From top to bottom: 2.9, 5.0, 12.0, and 21.2 mm SL. (From Ueyanagi, 1959, 1963a.)

follows: ". . . the profile of head, tip of snout and center of eye are on a nearly equal level" (Ueyanagi, 1963a). In addition, the shape (arrangement) of the pterotic and preopercular spines is diagnostic for larval identification (Ueyanagi, 1974).

On the vertical distribution of billfish larvae, Ueyanagi (1964) indicated that larvae appear to be distributed most abundantly in the surface layer during the daytime and vertical, diurnal migration seems to occur in the upper 50 m of waters (Table 3.). Billfish larvae appear from time to time in the stomach contents of the larvae and juveniles of sailfish and swordfish, *Xiphias gladius* (Arata, 1954; Gehringer, 1956). It is assumed that striped marlin larvae are therefore preyed upon by many surface feeding species, including the billfishes. Considering the very large numbers of eggs spawned by the striped marlin (see 3.15), it appears that mortality at the larval stage is extremely high.

Time of first feeding: No direct information is available. There is an observation that five copepods were seen in the stomach of a 3.9-mm sailfish larva (Gehringer, 1956).

Type of feeding: There is no information pertaining to the larvae of striped marlin. Of the larvae of sailfish in the Atlantic, Gehringer (1956) noted that "copepods constituted the food of specimens less than 6 mm. long. At this size fish larvae also were eaten, and no specimen exceeding 13 mm. had copepods in its stomach." Furthermore, it is also known that sailfish larvae have consumed istiophorid larvae half as long as their own body length. It is believed that the larvae of striped marlin, like the sailfish, begin to feed on fish larvae after reaching a size of about 7 mm.

Table 3.—Comparison of numbers (and percentage) of tows from which istiophorid larvae were captured, showing the various depths and times of towing, in the western Pacific area. (From Ueyanagi, 1964.)

Depth (m)	32 day tows		31 night tows	
	Number	Percent	Number	Percent
0	22	68.8	12	38.7
ca. 20	8	25.0	12	38.7
40-50	2	6.2	10	32.3

3.23 Adolescent phase

Nakamura (1968) described the juveniles of striped marlin based on two specimens collected from the South Pacific and the western Indian Ocean (see 2.21). His drawing has been reproduced as Figure 4. In the juvenile stage the snout is very elongate and, in fact, is longest at this stage relative to body length. The shape of the first dorsal fin still differs from the adult configuration, being highest anteriorly and decreasing gradually in height posteriorly. The arrangement of the viscera is similar to that of the adult. Nakamura also mentioned that the juvenile of striped marlin is similar to that of the white marlin in many respects except that the former has no ocelli on the first dorsal fin.

It is believed that large, powerful pelagic fishes such as tunas, billfishes, dolphins, etc., are the principal predators of juvenile striped marlin.

Little is known about parasites in juvenile striped marlin.

Immature striped marlin (80-100 cm eye-fork

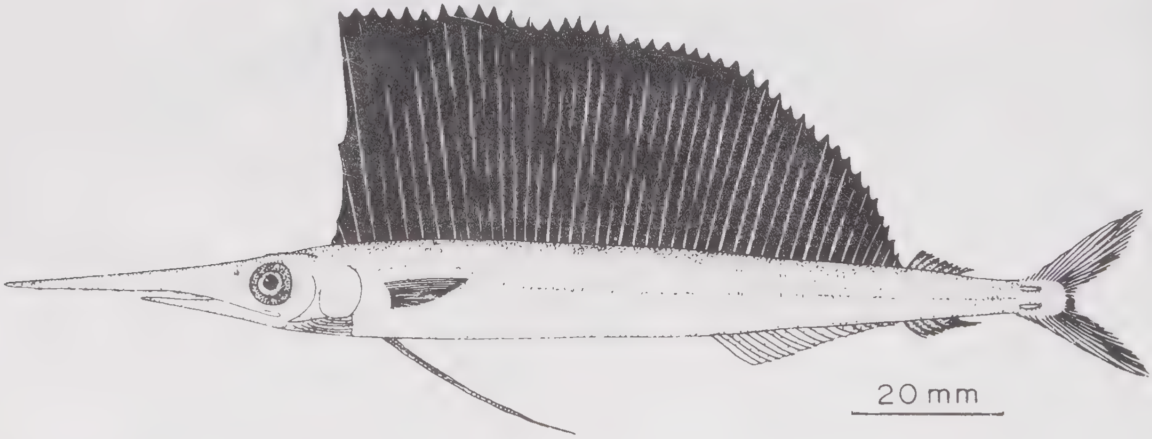


Figure 4.—Juvenile striped marlin (121.5 mm body length) collected from the southwestern Indian Ocean. (From Nakamura, 1968.)

ength) are taken by longline. The shape of the first dorsal fin in these fish differs from the adults in that the posterior rays are still high (Ueyanagi, 1957b). Fish and squid are found in the stomachs, as in the adults.

Following the 1954 hydrogen bomb test in Bikini, it was reported that virtually all of the radioactively contaminated striped marlin found in the northwestern Pacific were fish under 130 cm long (Anon., 1955). It is not clear what the implications are with respect to ecological differences between young and adult fish.

3.3 Adult Phase (Mature Fish)

3.31 Longevity

The ability to determine age of individual striped marlin has not been developed and thus life tables cannot be developed and life expectancy and maximum age are unknown.

Koto (1963a), using size-frequency data from western Pacific catches, was able to discern six age classes (which he designates as *n* though *n* + 5) in fish greater than 100 cm eye-fork length. The Walford growth transformation of his data indicated an ultimate size of about 290 cm. Specimens of this size are apparently occasionally taken in the South Pacific (Honma and Kamimura, 1958). From the general pattern of growth indicated by Koto, fish of this size would be expected to be at least 10 yr old.

3.32 Hardiness

Very little is known. Because of the large size and activity of this species, physiological experimentation is difficult. The return rate for tagged fish is much higher for striped marlin than for sailfish (Squire, 1974), and this may indicate greater general hardiness for striped marlin. Healing of severely broken bills (Wisner, 1958) may also be an indication of hardiness. Sportsmen usually report that the striped marlin fights harder than the sailfish when hooked and tends not to die as easily as the sailfish.

3.33 Competitors

The other billfishes, particularly the smaller species sailfish and probably the shortbill spearfish), sword-ish, and the larger tunas are probably the closest ompetitors for food. Even the smaller scombrids hare many forage species with the striped marlin. The dolphin and pelagic sharks such as *Prionace*, *Carcharhinus*, and *Isurus* utilize many of the same orage species (Parin, 1968). Striped marlin tend to eed more on epipelagic species and less on mesopelagic species than the oceanic tunas or the wordfish.

3.34 Predators

Predators of adults are probably extremely limited, the only likely candidates being some of the large pelagic sharks and the toothed whales.

Bills of billfishes have been found in floating objects and other fish. Occasionally bills of striped marlin are found to have been broken off, and the fish are known sometimes to ram fishing boats when hooked, but it is not certain that any of these occurrences have any relation to defense or aggressive action.

3.35 Parasites, diseases, injuries, and abnormalities

Parasites and diseases: The body surface usually harbors many caligoid copepods which frequently congregate on the ventral surface, particularly in the area around the anal fin and on the head. Williams (1967) reports they may occur in the thousands. The skin surface in areas of concentration often appears red and irritated. Penellid copepods (*Penella fillosa*) are frequently found penetrating the skin and anchored in the muscle or sometimes in internal organs such as the gonads. Koga (1967) reports the percentage occurrence of caligoid copepods and penellid copepods on striped marlin in Fiji waters was 100% and 20%, respectively. Eldridge and Wares (1974) report the percent occurrence of penellids above and below the lateral line on one side of the body as 26.2% and 22.8% with average infections of 3.3 and 2.3 copepods per fish. Stalked barnacles (*Conchoderma irgatum*) frequently are attached to the penellid copepods and often to the marlin skin, normally near the vent (Williams, 1967). Digenetic trematodes were reported found on the gills by Williams (1967). Monogenetic trematodes of the family Capsalidae are quite common on the surface of the skin (Eldridge and Wares, 1974).

Cestode worms resembling *Dibothrium manubriformes* have been found in the intestines and nematodes (*Contracaecum incurvum*) are very common in the stomach occurring in densities greater than 200 per stomach (Morrow, 1952b). The copepod, *Philichthys xiphiae*, has been found in the mucus canals of the preopercular and opercular bones, and capsalid trematodes are commonly found in the nasal capsule (Eldridge and Wares, 1974).

Injuries and abnormalities: Gastric ulcers were reported in 14% of 563 eastern Pacific striped marlin (Evans and Wares, 1972). These may be associated with the presence of nematodes (R. T. B. Iversen, Southwest Region, National Marine Fisheries Service, NOAA, Honolulu, Hawaii, pers. commun.). The small squaloid shark (*Isistius brasiliensis*), the probable cause of crater wounds on many pelagic fishes including istiophorids (Jones, 1971), probably parasitizes striped marlin.

There is evidently little ability for regeneration as broken bills and pelvic fins are seen to heal over rather than regenerate. Striped marlin have recovered after losing almost all of the bill (Wisner, 1958).

3.4 Nutrition and Growth

3.41 Feeding

Most active feeding probably takes place in the morning. LaMonte (1955) reported that squid found in the stomachs of striped marlin off Peru and Chile were less digested in fish caught in the morning than those landed after noon. Kobayashi and Yamaguchi (1971), examining only fish caught after noon, found a decline in feeding activity toward sunset. Williams (1967), however, suggests that East African fish feed at any time of the day or night.

Apparently the food is usually captured by grasping with the mandibles rather than by spearing, slashing, or clubbing with the bill. Fish which have lost the bill completely survived well. Some food specimens are occasionally found, however, which have been neatly speared (Wisner, 1958; Evans and Wares, 1972).

3.42 Food

Several authors have reported on food habits. Table 4 gives an idea of the variety of food species which have been found most important in different studies. It is notable that, despite the large size and lack of gill rakers in striped marlin, relatively small forage items are commonly taken (Nakamura, 1949).

Food habits do not appear to vary appreciably with sex or size over the range of sizes commonly caught. Considerable variation in species composition of the diet occurs, however, with season and geographic location (Evans and Wares, 1972). Such variations probably reflect variations in availability of the food organisms in keeping with the generally accepted concept that these fish are broadly carnivorous, nonselective feeders. This is true of epipelagic fishes generally (Parin, 1968).

The average volume of food found in stomachs of striped marlin caught by the eastern Pacific sport fishery ranged from 14 to 23 fluid ounces per stomach (Evans and Wares, 1972). Yamaguchi (1969) reports that empty stomachs were found in 66% of striped marlin caught by longline. This percentage tends to be larger in billfish than in tunas. Evans and Wares (1972) found 19% empty stomachs.

3.43 Growth rate

Weight-frequency modal progressions in Hawaii landing data suggest an annual growth rate of about 30 pounds (Royce, 1957). Merrett (1971) found agreement with Royce's data in size-frequency distributions from East Africa. Possible modal lengths of about 152, 167, 177, and 197 cm eye-fork length were found in the length-frequency distribution for the total catch. Computed weights at modal lengths gave annual weight increments of 27, 21, and 23 pounds.

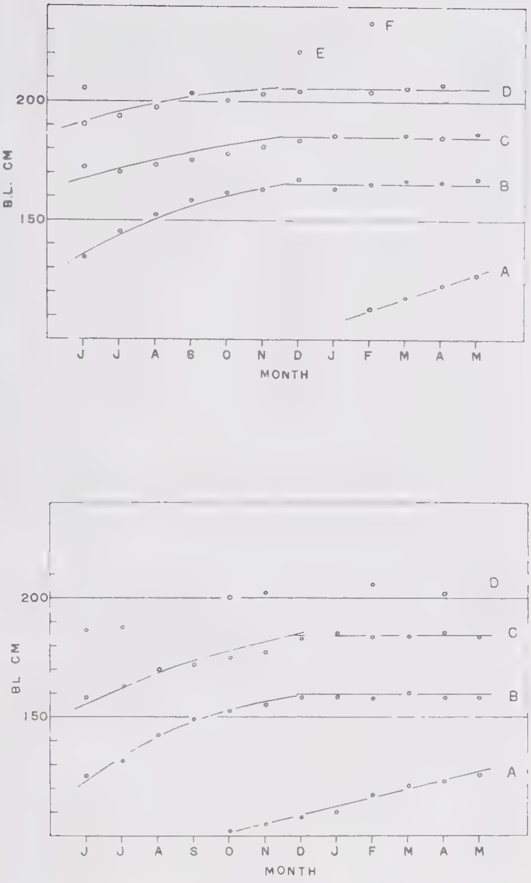
Table 4.—Some reported major food species for striped marlin.

Area	Food species	Author
East Africa	*Fistularia* sp. *Auxis* sp. Squid	Williams, 1967
New Zealand	*Scomberesox saurus* *Arripis trutta* *Loligo* sp.	Morrow, 1952b
New Zealand	*Ommastrephes sloani* *Caranx lutescens* *Scomber japonicus*	Baker, 1966
Tasman Sea	*Alepisauridae* *Clupeidae*	Koga, 1968
Bonin Islands	*Gempylus* sp. Cephalopods *Pseudoscopelus* sp. *Alepisaurus* *Ostracion* Crustacea	Yabuta, 1953
California	*Cololabis saira* *Engraulis mordax* *Sardinops caerulea*	Hubbs and Wisner, 1953
California	*Engraulis mordax* *Trachurus symmetricus*	Evans and Wares, 1972 Craig, 1972
Mazatlán, Mexico	Squid *Etrumeus teres* *Fistularia* *Argonauta* sp.	Evans and Wares, 1972
Baja California, Mexico	Squid *Etrumeus teres* *Scomber japonicus* *Fistularia* sp.	Evans and Wares, 1972
Peru-Chile	Squid	LaMonte, 1955
Chile	*Engraulis ringens* *Trachurus symmetricus* Squid	de Sylva, 1962

Koto (1963a) working with length-frequency data from the western North Pacific, found six modal groups (n though $n+5$). The monthly progression of these modes is shown in Figure 5. The designations of these modal groups are as follows:

Group	*Lengths* (cm)	*Increment* (cm)
n	100-120	?
$n+1$	120-160	35
$n+2$	160-185	27
$n+3$	185-205	19
$n+4$	205-220	16
$n+5$	220-233	13

There is a marked seasonal change in growth rate with rapid growth occurring from June to November and very little growth in the remainer of the year for age groups $n+1$, $n+2$, and $n+3$. Age group n appears



igure 5.—Seasonal changes in modes derived from average ear's length frequencies of longline-caught striped marlin. A. orth Pacific Current area; B. East China Sea (long. 120°-30°E). (From Koto, 1963a.)

n the catch only after September, as fish larger than 00 cm and shows rapid growth right through the winter. The failure of the fishery to capture many fish elow 100 cm makes it impossible to say what the absolute ages of the groups are.

The annual growths of the $n+1$ and $n+2$ age groups differ between areas and years. Koto (1963b) showed that in the North Pacific Current area the yearly differences in the length composition were caused by differences in the average length of the $n+1$ age group. In the North Equatorial Current area, however, these differences were probably caused by differences in age composition and the relative abundance of the n and $n+1$ age groups.

Koto (1963b) has shown growth rate to be affected y population density. The very close inverse elationship between growth of the $n+1$ age group and he total fish abundance, or especially the abundance of the n and $n+1$ groups is shown in Figure 6. The correlation coefficients between growth of the $n+1$ age group and total fish abundance were −0.958 (df = 6) for the North Equatorial Current area and −0.737 (df = 8) for the North Pacific Current areas.

Royce (1957) suggested the maximum size reached by striped marlin is less than 226.8 kg (500 pounds). Records were given as follows: 172.8 kg (381 pounds) off New Zealand; 142.4 kg (314 pounds) from Pacific equator; a "questionable" record of 196.9 kg (434 pounds) from the Hawaiian market, where normally only occasional specimens approach 136.1 kg (300 pounds); a somewhat questionable record because of possible confusion with the blue marlin of 219.1 kg (483 pounds) from Chile; the world's record, taken off California, was 692 pounds, which was based on a misidentified blue marlin.

The theoretical maximum length of about 290 cm mentioned in section 3.31 is equivalent to 259.5 kg (572 pounds). A fish of 290 cm was taken by longline in the South Pacific (Honma and Kamimura, 1958).

Average semimonthly condition factors (K) computed

$$K = \frac{W \times 10^5}{L^3}$$

where W is whole fish weight in kg
L is eye-fork length in cm

for eastern Pacific fish ranged approximately from 0.80 to 1.26 (Eldridge and Wares, 1974).

In the East China Sea, condition factor

$$K = \frac{W}{L^3}$$

where W = gilled and gutted weight in kan (= 3.75 kg)
L = eye-fork length in m

was found to increase with body length from about 8 at 110 cm to a peak of about 10 at 180 cm and then to decline to about 9 with larger fish up to 230 cm

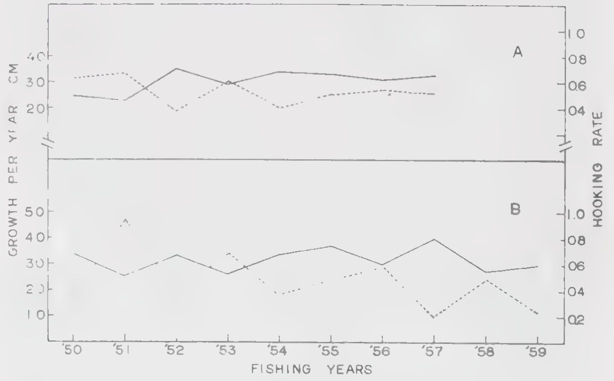


Figure 6.—Relation between total fish abundance and growth of the $n+1$ age group. A North Equatorial Current area; B. North Pacific Current area. —— growth per year; ……hook rate. (From Koto, 1963b.)

(Furukawa et al., 1958). The condition factor also showed a seasonal drop from about 10.8 in December to about 8.7 in June for fish of body length 166-195 cm. The drop in condition factor before June was much more abrupt than the increase after June. A similar seasonal cycle was also apparent for fish of 136-165 cm.

3.44 Metabolism

There are no data on metabolic rates for this species. Lindsey (1968) found body muscle temperatures as much as 2.6°C higher than the surrounding seawater. The highest temperature recorded occurred near the center of the epaxial muscle mass with a lesser maximum slightly below the hypaxial muscle mass center. Red muscle was found to be lower than white muscle at comparable depths beneath the skin. Temperatures of the viscera exceeded seawater temperatures by 0.7-1.3°C.

Barrett and Williams (1965) report the mean hemoglobin content in 16 striped marlin was 11.3 ± 0.75 g Hb/100 ml and ranged from 5.8 to 16.8.

3.5 Behavior

For feeding behavior, see 3.41; for reproductive behavior see 3.13, 3.21.

3.51 Migrations and local movements

See also 2.22 and 2.3.

The migration pattern of striped marlin appears to be principally a simple latitudinal movement between spawning areas and productive feeding areas (Parin, 1968). The movement is toward higher latitudes in the summer of each hemisphere and back toward equatorial waters in winter. In the northern hemisphere the peak of the northward migration is August-September and the southward migration begins in October and continues through February. The northward movement is also accompanied by an eastward expansion in the eastern Pacific (Howard and Ueyanagi, 1965; Fisheries Agency of Japan, Research Division, 1969-72).

In the central North Pacific small fish of about 13.6 kg (30 pounds) appear in Hawaii in winter, grow to 22.7-27.2 kg (50-60 pounds) by May or June, then migrate north for several months, and return to Hawaii as larger fish the next year. A similar pattern of migration is common to areas west of long. 180° (Howard and Ueyanagi, 1965).

In the southern hemisphere west of long. 150°W fish migrate north from south of lat. 30°S from August through November and form concentrations which are exploited in the area lat. 18°-19°S. The period of this migration corresponds to the spawning season. After November the fish appear to migrate south (Koga, 1967).

In the eastern South Pacific a high density area, which occurs in the area lat. 10°-17°S, long. 90°-115°W during the second and third quarters, appears to move southwest to the region of lat. 20°-28°S, long. 100°-110°W in the fourth and first quarters (Kume and Joseph, 1969a, b).

In the eastern North Pacific the seasonal north-south movements are apparent but less pronounced. Striped marlin do occur in their extreme northern range (southern California) during late summer and fall when surface temperatures reach a peak, but it is not clear whether these fish have come from the south or from the west (Howard and Ueyanagi, 1965). Data from fish tagged in the sport fisheries of southern California and Mexico provide evidence that striped marlin are capable of fairly long migratory movements up to 3,000 miles (Fig. 7). Some fish do move from California southward to the tip of Baja California and further, but there is no evidence of migration from Mexican waters to southern California (Squire, 1974).

Howard and Ueyanagi (1965) suggested on the basis of the appearance of an unusually small size group in California in 1958 and subsequent appearance 2 yr later of a small group in New Zealand, which was of a size expected for fish 2 yr older than the former, that there may be transpacific interchange between these remote areas.

Following the 1954 hydrogen bomb test in Bikini, contaminated fish were found only from the North Pacific, suggesting the possibility of separate populations in the two hemispheres (Nakamura, 1969).

In addition to the primary migratory trend, there are also lesser local movements reported. The area of high density off the central Mexican coast generally tends to expand westward seasonally reaching its maximum westward extent at about long. 130°W during the fourth quarter of the year (Kume and Joseph, 1969a, b). The region of high density around the Galapagos Islands during the second and third quarters expands eastward to the coast of Ecuador during the fourth and first quarters (Kume and Joseph, 1969a, b; Kume and Schaefer, 1966).

Nakamura (1949) mentions dense schools move from south to north along the coast of Vietnam in March and April.

In the western Pacific, Furukawa et al. (1958) report a gradual westward migration of fish from the vicinity of the Bonin Islands to the East China Sea in July and August where they stay until November after which a southward emigration takes place.

Migratory patterns in the Indian Ocean are unknown. The seasonal increase in density off East Africa during the northeast monsoon is believed to be a postspawning feeding migration (Williams, 1967; Merrett, 1971). The north-south type of seasonal movements that are typical in the Pacific are most evident off South Africa. A northward movement in the springtime (second quarter) is evident in the

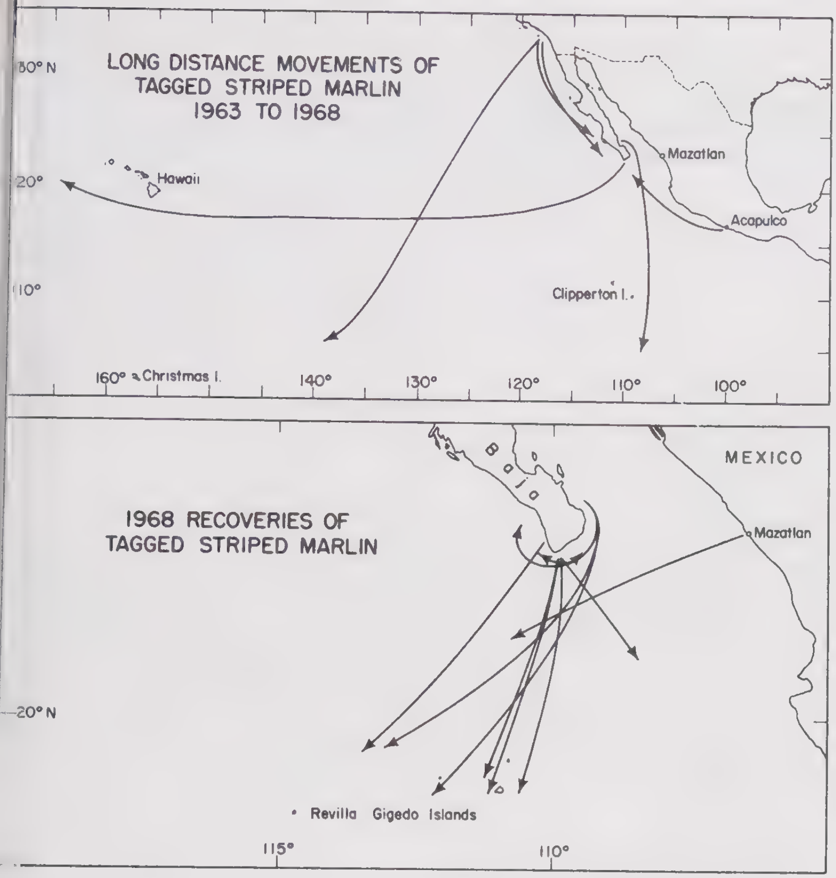


Figure 7.—Movements of tagged striped marlin in the eastern Pacific Ocean.

western Arabian Sea (Fisheries Agency of Japan, Research Division, 1969-72).

3.52 Schooling

Striped marlin, like the other istiophorids, do not rm dense schools like the tuna, and the individuals re usually dispersed at wide intervals (Nakamura, 949). Frequently, however, several fish are seen together; sometimes following one another, especially during the spawning season.

Surfacing is apparently more common when the wind and waves are high. When wind and current are moving in the same direction, the surface is calm and few fish are seen at the surface. When the wind runs counter to the current, high waves result, and fish are most often seen at the surface and are usually swimming in the direction of the wind, at least in Formosan waters (Nakamura, 1938).

When surfaced, the striped marlin usually is swimming very slowly with the upper caudal lobe above the surface and the dorsal fin retracted and not showing. This characteristic reportedly distinguishes them from swordfish which are unable to depress the dorsal fin and show both the dorsal and caudal fins when surfaced. Striped marlin swim faster and are less easily approached when surfaced than the swordfish (Philippi, 1887).

Little is known about how far the fish move vertically. Saito et al. (1972) report that striped marlin have been caught at 150- to 290-m depths by vertical longline experiments in Fiji waters.

For composition of stocks by size see also section 2.22. As mentioned previously, there is considerable variation in size composition between various regions and particularly between the northern and southern groups in the Pacific (see, for example, Howard and Ueyanagi, 1965; Koga, 1967; and Kume and Joseph, 1969b). As mentioned earlier, southern fish tend to be larger than northern fish throughout the Pacific. Size composition of striped marlin in the Indian Ocean resembles the North Pacific size distribution more than the South Pacific.

Striped marlin "schools" occur in waters in common with the schools of most of the Indo-Pacific scombroids, particularly albacore, yellowfin tuna, and bigeye tuna, *Thunnus obesus*.

3.53 Responses to stimuli

Very little is known of this subject as it relates to striped marlin. The possible response to temperature has been mentioned previously. It may be pertinent to note here that when billfishes are caught by hook or harpoon, they first make several leaps into the air and then swim wildly in broad circles near the surface. Tunas, on the other hand, try to escape in a vertical direction by diving deep (Nakamura, 1949).

4 POPULATION

4.1 Structure

4.11 Sex ratio

Sex ratio of the population as a whole is unknown; but from the data of Williams (1967), Kume and Joseph (1969b), and Merrett (1971), females usually predominate in longline catches. The notable exception to this is on the spawning grounds, where males tend to predominate (Kume and Joseph, 1969b). The percentage of females tends to increase with size of fish (Kume and Joseph, 1969b). There is a tendency for spawning grounds to be dominated by larger fish than in nonspawning areas.

4.12 Age composition

Since age determination of individual fish is not possible at present, age composition of the population has not been studied. See 3.43 on growth rate.

4.13 Size composition

Size composition varies greatly between stocks and with seasons (see 3.52).

Size at first capture by tuna longline gear is about 80 cm eye-fork length.

Size at first maturity is between 140 and 160 cm eye-fork length.

Maximum size is probably about 290 cm eye-fork length or 258.6 kg (570 pounds).

See 1.31 for length-weight relationships.

4.2 Abundance and Density (of Population)

4.21 Average abundance

No data.

4.22 Changes in abundance

Relative abundance in terms of average CPUE (catch per unit of effort) for major ocean areas is shown in Table 5 for the years 1962-70. These data show no apparent trend for the eastern, northern or the Pacific Ocean at large, however, there is a general decline noted for the South Pacific and a slight decline in the Indian Ocean, the latter since 1966 (Fisheries Agency of Japan, Research Division, 1965-72).

Year-to-year changes in CPUE for the various

Table 5.—Catch statistics by major ocean areas of Japanese longline fishery for striped marlin for 1962-1970 (Fisheries Agency of Japan, Research Division, 1965-72).

	1962	1963	1964	1965	1966	1967	1968	1969	1970
Indian Ocean									
E[1]	68.4	57.3	68.9	79.9	89.6	126	119	101	78
C[2]	48	34	38	81	106	114	63	59	45
CPUE[3]	0.07	0.06	0.06	0.10	0.12	0.09	0.05	0.06	0.06
Whole Pacific									
E	290	337	283	288	301	306	286	306	282
C	287	338	508	421	351	406	506	323	450
CPUE	0.10	0.10	0.18	0.14	0.12	0.13	0.18	0.11	0.16
North Pacific									
E	156	154	140	153	150	193	165	169	163
C	144	123	210	156	98	159	154	101	242
CPUE	0.09	0.08	0.15	0.10	0.06	0.08	0.09	0.06	0.15
South Pacific									
E	109	131	81.2	92.2	104	70.6	71.0	70.1	67.7
C	59	49	28	29	30	17	14	14	32
CPUE	0.05	0.04	0.03	0.03	0.03	0.02	0.02	0.02	0.05
Eastern Pacific (E of 130°W)									
E	24.7	52.1	62.0	43.6	47.5	42.4	50.4	67.2	52.1
C	84	166	270	236	223	230	338	208	177
CPUE	0.34	0.32	0.44	0.54	0.47	0.54	0.67	0.31	0.34

[1] E = Effort in hooks $\times 10^6$.

[2] C = Catch $\times 10^3$.

[3] CPUE = Catch/100 hooks.

gions of the Pacific and Indian oceans are examined section 5.41.

Seasonal variations in available stock are marked. ee 2.22 on differential distribution. Kume and oseph (1969a) have shown that there is a threefold easonal fluctuation in CPUE for the various regions the eastern Pacific.

4.23 Average density

No data.

4.24 Changes in density

No data.

4.3 Natality and Recruitment

4.31 Reproduction rates

Annual egg production rates have not been esimated. Little is known of fecundity relationship with fish size. See 3.15 for some estimates.

Nothing is known of survival rates of eggs and larvae because they are so rarely collected.

4.32 Factors affecting reproduction

No data.

4.33 Recruitment

There is little information pertaining to the variation in annual recruitment (see 3.43 and 4.24).

4.4 Mortality and Morbidity

No work has been done on mortality rates or causes of mortality.

4.5 Dynamics of Population (as a Whole)

No work has been done.

4.6 The Population in the Community and the Ecosystem

There is no specific information on this subject available; some general information on distribution and life history is presented in sections 2 and 3.

5 EXPLOITATION

5.1 Fishing Equipment

5.11 Gear

Virtually all of the commercial catch of striped marlin is by longlining. The harpoon fishery for billfishes is responsible for less than 5% of the total catch.

The longline gear aims largely at tunas and billfishes which are distributed at depths of around 100-150 m. The gear consists of mainline, float lines, branch lines, hooks, and buoys. The construction of the longline gear differs according to the species of fish sought, but Morita (1969) presents an example of a "standard" gear (Table 6). Several hundred of these units (each unit is referred to as a "basket") are joined in a series to make up a set. The gear is retrieved with a longline hauler.

Suda and Schaefer (1965) gave examples of the various types of longline gear presently in use (Table 7), and indicated that types 1 through 5 are the more typical ones in use. They also included the estimated hook depths for the different types of gear.

Billfishes are generally found closer to the sea surface than tunas. Therefore, in fishing primarily for billfishes, the longline gear is modified by shortening the float line and the branch lines and also by adding another buoy in the middle of the mainline section, the latter bringing the hooks closer to the surface. Furukawa et al. (1957) reported that for fishing billfishes in the East China Sea, the combined length

Table 6.—General form of tuna longline. (From Morita, 1969.)

Name of part	Material	Length	Number used for 1 basket
Mainline	Cremona (20S, 55×3×3)	250 m[1]	1
Branch line	Cremona (20S, 55×3×3)	11 m	4
Sekiyama	Steel wire (27 # 3×3) and hemp yarn coiled with thread No. 5)	5.5 m	4
Kanayama	Steel wire (27 #, 3×3, Type M)	3 m	4
Hook	Steel	3.8 sun[2]	4
Float Line	Cremona (20S, 55×3×3)	22 m	1
Flag buoy	Flag, bamboo, float (glass ball or synthetic resin ball)	—	1
Radio buoy			2 or 3 (for all basket)

[1] Length per one basket.

[2] 1 sun = 3.03 cm.

Table 7.—Some examples of Japanese tuna longline gear. (From Suda and Schaefer, 1965.)

Type no.	1	2	3	4	5	6	7	8
A. The structure of one basket of the line (unit of length: meters)								
Length of mainline	300	300	300	300	300	245	360	350
Length of branch line								
Cotton or vinyl rope	13.5	10.5	12.0	11.5	12.0	12.0	14.5	12.0
Ganged wire leader	6.0	6.0	8.0	6.0	7.0	8.0	7.0	7.0
Wire leader	1.5	2.0	2.5	1.5	2.0	2.0	3.5	2.5
Length of float line	18.5	19.5	20.0	16.5	22.0	18.0	22.5	25.0
Number of hooks	5	5	5	5	5	4	4	6
B. The estimated maximum depth of each hook of the lines shown above								
No. 1 hook	86.5	85.0	89.5	82.5	90.0	84.5	113.5	92.5
2	127.5	126.0	130.5	123.5	131.0	123.0	169.5	136.5
3	148.5	147.0	151.5	144.5	152.0	123.0	169.5	168.5
4	127.5	126.0	130.5	123.5	131.0	84.5	113.5	168.5
5	86.5	85.0	89.5	82.5	90.0			136.5
6								92.5

of the float line and branch line should not exceed 30 m.

As for the amount of gear fished per day, Yoshida (1966) reported that "Vessels of 39 to 99 gross tons fish 210 to 355 baskets; vessels 100 to 190 gross tons fish 355 to 400 baskets; and vessels 200 to 500 tons fish 400 to 450 baskets." Suda and Schaefer (1965) reported that Japanese vessels in the eastern Pacific fished an average of 2,000 hooks (about 400 baskets) per set.

The basic construction of the longline gear has remained unchanged over the years. However, due to manpower problems some effort has been directed towards developing laborsaving devices in longlining. Two examples are the reel-type and tub-type of longlining.

In the reel-type, the mainline is continuously reeled onto a drum, while in the tub-type, the retrieved line is coiled into a large tub. Important advances in addition to the line hauler, include the "slow-conveyor" (for line setting and line hauling), the "guide stand" and "guide roller" (for leading line), gear-transporting conveyor system, line-winder system, etc. In using these methods, the branch lines are joined to the mainline by the use of snaps (Katsuo-Maguro Nenkan, 1969).

The principal bait used in longlining is frozen Pacific saury, *Cololabis saira.* Squid is also commonly used. Mackerel, *Scomber* sp., as well as mackerel scad, *Decapterus* sp., have been used as alternate bait. In addition, experiments are underway to utilize silver carp, *Hypophthalmichthys molitrix*, as well as artifical preparations (e.g., infused with extracts of saury) as longline bait.

Depending on the location, certain baits have been reported to have advantages in catching billfishes. For instance, in the East China Sea fishing grounds, live mackerel were believed effective and were used extensively. However, Furukawa et al. (1957) reported that using live or dead mackerel did not significantly affect the catches of white marlin (= black marlin), striped marlin, and broadbill.

The main piece of equipment in the harpoon fishery is the harpoon itself. The harpoon pole of oak is about 4 m long and at its tip is a three-pronged iron piece about 7 mm in diameter. The detachable harpoon of steel about 10 cm in length, connected to about 100 m of line, is placed over this iron tip. Recently the electric harpoon has been used in order to kill the fish quickly. When the harpoon enters the fish, a wire distributed along the harpoon line is charged with electricity.

5.12 Boats

The longline vessels fishing in the Indian and Pacific oceans for striped marlin are largely those from Japan. Other vessels are from Taiwan and Korea.

The details on the construction of longline vessels are given by Kanasashi (1960) and by Yoshida (1966). There are two types of longline vessels: those that use longline exclusively and those that use both longline and pole and line. The holds on longline vessels are not divided into small compartments to carry live bait. Thus, the hold space in the longliners is 20% to 40% greater than in the combination vessels.

Longline vessels are constructed of wood or steel; those larger than 100 gross tons are usually constructed of steel. Most of the longliners are 250 to 350 gross tons; at this stage of the fishery they appear to be the most economical and efficient size to operate. The specifications of typical longliners of this size class and those of some typical combination vessels are given in Yoshida (1966).

Other than the independently operating vessels, there is the mother ship operation in which several catcher boats are transported on the deck of a mother ship to the fishing grounds.

Small mother ships of 400 to 800 gross tons are able to carry only one portable catcher boat, but the larger 1,000- to 3,000-ton mother ships carry six catcher boats. The portable catcher boats measure about 15 m in length (Yoshida, 1966). To decrease the weight of the portable boats, recent constructions have been of fiber-reinforced plastic (FRP). The weight of a FRP boat is about 13 tons, or approximately two-thirds the weight of former catcher boats (Kazama, 1967).

Significant advances have also been made in preserving the catch of high-quality sashimi fish. Many vessels are equipped with refrigeration equipment capable of preserving the catch at very low temperatures of −40° to −45°C. In this way, the vessels are able to deliver fish in excellent condition and as a result, billfish prices have increased greatly in the Japanese market.

In addition, there have been advances in automating ship operations, fishing gear, and other equipment. Almost all longliners are equipped with fish detectors. Living conditions on the ships have also been improved considerably, and many vessels are now equipped with air conditioning for the crew's comfort (Katsuo-Maguro Nenkan, 1969).

Harpoon vessels are constructed with an extended prow where the harpooner is stationed. These vessels are constructed of wood, and range in size from about 10 to 40 tons. Billfishes taken by these vessels are kept on ice for delivery to the market.

5.2 Fishing Areas

5.21 General geographic distribution

The longline fishery now virtually covers the entire distribution of the species (see 2.1 and 2.22). The major sport fishing areas are southern California, Mexico, Panama, Ecuador, Peru, Chile, Hawaii, Tahiti, Fiji, New Zealand, Australia, and East Africa (not listed in order of importance).

5.22 Geographic ranges

See also 5.41.

Longlining is carried out across the high seas to within 5 miles of coastlines in places. The sport fishery is generally restricted to within about 75 miles of coastlines with the bulk of the fishing much closer.

The greatest fishing pressure is exerted in the North Equatorial Current in the Pacific and western Indian oceans, in the Kuroshio and Kuroshio extension, in the North Pacific Gyral northeast of the Hawaiian Islands, in the South Equatorial Current from about long. 90° to 140°W, and also off Mexico and Ecuador.

Regarding the development of the Japanese longline fishery, Suda and Schaefer (1965) report that prior to about 1952 the fishery was confined to the western and central Pacific. After this date it expanded into the Indian Ocean extending west of long. 80°E in 1954 and throughout the Indian Ocean by the end of 1955. In the Pacific, the fishery expanded eastward between lat. 10°N and lat. 10°S reaching 130°W by late 1956 and long. 85°W by 1961. After 1963 the fishery in the eastern Pacific expanded rapidly poleward, the northward expansion being primarily for striped marlin (Kume and Joseph, 1969a).

The fishing grounds for the Japanese harpoon fishery are located in the waters of Sanriku (off northeast of Honshu), around Izu, and East China Sea.

5.23 Depth range

Little has been written regarding fishing effort by depth range. Merrett (1968a) reports almost half of the striped marlin caught during experimental longlining off East Africa were caught over less than 1,000 fathoms even though most of the effort was expended beyond this depth contour.

5.24 Conditions of the grounds

See sections 2.1, 2.2, and 2.3.

5.3 Fishing Seasons

For sections 5.31, 5.32, and 5.33 see section 2.22.

The fishing season for the Japanese harpoon fishery in the waters of the Sanriku fishing ground extends from June to November with the peak occurring from July through September; in the Izu area from December to August with its peak from February through April; and in the East China Sea from December to February.

5.4 Fishing Operations and Results

5.41 Effort and intensity

Type of unit of effort: Detailed data on fishing effort and catch in the Japanese tuna longline fishery are published in the "Annual report of effort and catch statistics by area on Japanese tuna longline fishery" by the Research Division, Fisheries Agency of Japan. Fishing effort is reported in terms of number of operations and number of hooks fished; catch is reported in terms of number of fish. The statistics are reported on a monthly basis by 5° units.

Since 1967, Taiwan has also begun to publish data from their tuna longline fishery, following the same format as the Japanese publication. The Taiwan data are published annually in "Report on survey of production and marketing of Taiwan's tuna longline fishery" by the Taiwan Fisheries Bureau. Publication of effort and catch statistics of the Korean longline fishery started in 1970 in "Yearbook of catch and effort statistics on Korean tuna longline fishery" issued by the Office of Fisheries, Korea.

Landings per unit of fishing effort: As noted above, the catch statistics are reported in terms of numbers of fish taken in the various unit areas. Landings by weight can be estimated from the data along with average body weight data.

Catches per unit of fishing effort: The catch per unit of effort (CPUE) can be obtained in terms of catch in numbers per 100 or 1,000 hooks fished. Strasburg (1970) studied year-to-year changes in CPUE of billfishes in the Pacific by analyzing the 1953-63 Japanese longline data for quadrangles measuring 20° of latitude and longitude. He noted a progressive decline over the years in the CPUE for the striped marlin of western and central South Pacific (lat. 20°-40°S) areas. Strasburg (1970) concluded that while some workers have attributed the decline in CPUE to heavy fishing, "It is impossible to determine its real cause without more information on various biological features related to migration, reproduction, age, and year classes."

Honma and Suzuki (1969) studied the apparent abundance of striped marlin in the principal fishing grounds in the Pacific (northwestern Pacific, eastern Pacific, and waters east of Australia) for the years 1960-66. They noted no apparent trends in CPUE in the northwestern Pacific and eastern Pacific grounds. On the other hand, for waters east of Australia, they reported a definite decreasing trend; the CPUE has been at a low level of around 0.1 fish per 100 hooks since 1964.

Of the striped marlin in the Indian Ocean, Kikawa et al. (1969) examined the annual changes in CPUE (number of fish per 1,000 hooks) based on data for the years 1962-67. They reported CPUE of about 0.6 fish per 1,000 hooks between 1962 and 1964, followed by an increase to about 1.0 in 1965-67. The authors concluded that "An increasing trend in the CPUE for striped marlin in this period may probably represent the increase in effectiveness in catching fish."

Fishing effort per unit area: Figure 8 shows the distribution of fishing effort of the Japanese tuna longline vessels in 1970. The effort, in terms of numbers of hooks fished, is shown by 5° quadrangles.

If we examine the data along with catch per unit area data of striped marlin (Fig. 9) it is apparent that the relatively large fishing effort in the eastern Pacific off Mexico and Ecuador is principally related to pursuit of striped marlin in those areas.

Total fishing intensity: The total fishing effort of the Japanese longline vessels in recent years (1965-69) for the Pacific and Indian oceans is estimated at about 400 million hooks fished per year. The efforts by areas are given in Table 5 (see 4.23).

Since 1963 there has been a significant increase in fishing effort in the eastern Pacific region. Correspondingly the fishing grounds for striped marlin also has increased during this period.

In the South Pacific region, however, effort has decreased from about 100 millin hooks in 1965-66 to around 70 million hooks beginning in 1967.

5.42 Selectivity

Small striped marlin under 80 cm eye-fork length are virtually never taken by longline.

Furukawa et al. (1958) have reported that striped marlin taken by harpooning in the East China Sea fishing grounds are relatively heavier (higher fatness index) than fish taken by longline.

5.43 Catches

Total annual yields: The FAO "Yearbook of fishery statistics" reports the total annual yields of striped marlin; Table 8 summarizes the 1970 catch (FAO, 1971). The recent total annual landings of striped marlin have been around 25,000 tons from the Pacific and Indian oceans.

Total annual yields from different fishing grounds: As seen in Table 8, the striped marlin catches are high in the eastern Pacific; the catch from this area comprises about one-half of the total Pacific

Table 8.—Catches of striped marlin by fishing areas for 1964-70. (From FAO, 1971.)

Area	1964	1965	1966	1967	1968	1969	1970
	In thousands of metric tons						
Indian Ocean	(2.4)	(3.8)	(3.8)	(6.2)	(3.8)	(4.3)	(3.1)
Western	1.2	2.1	3.2	4.9	2.2	2.5	2.1
Eastern	1.2	1.7	0.6	1.3	1.6	1.8	1.0
Pacific Ocean	(25.6)	(22.5)	(20.5)	(19.5)	(21.6)	(20.5)	(22.1)
Northwest	8.6	8.8	7.0	6.9	7.2	8.5	8.4
Eastern central	14.0	11.3	9.1	10.4	11.0	8.7	10.9
Southwest	1.4	1.3	2.3	0.9	1.7	1.6	1.6
Southeast	1.6	1.1	2.1	1.3	1.7	1.7	1.2
Total	28.0	26.3	24.3	25.7	25.4	24.8	25.2

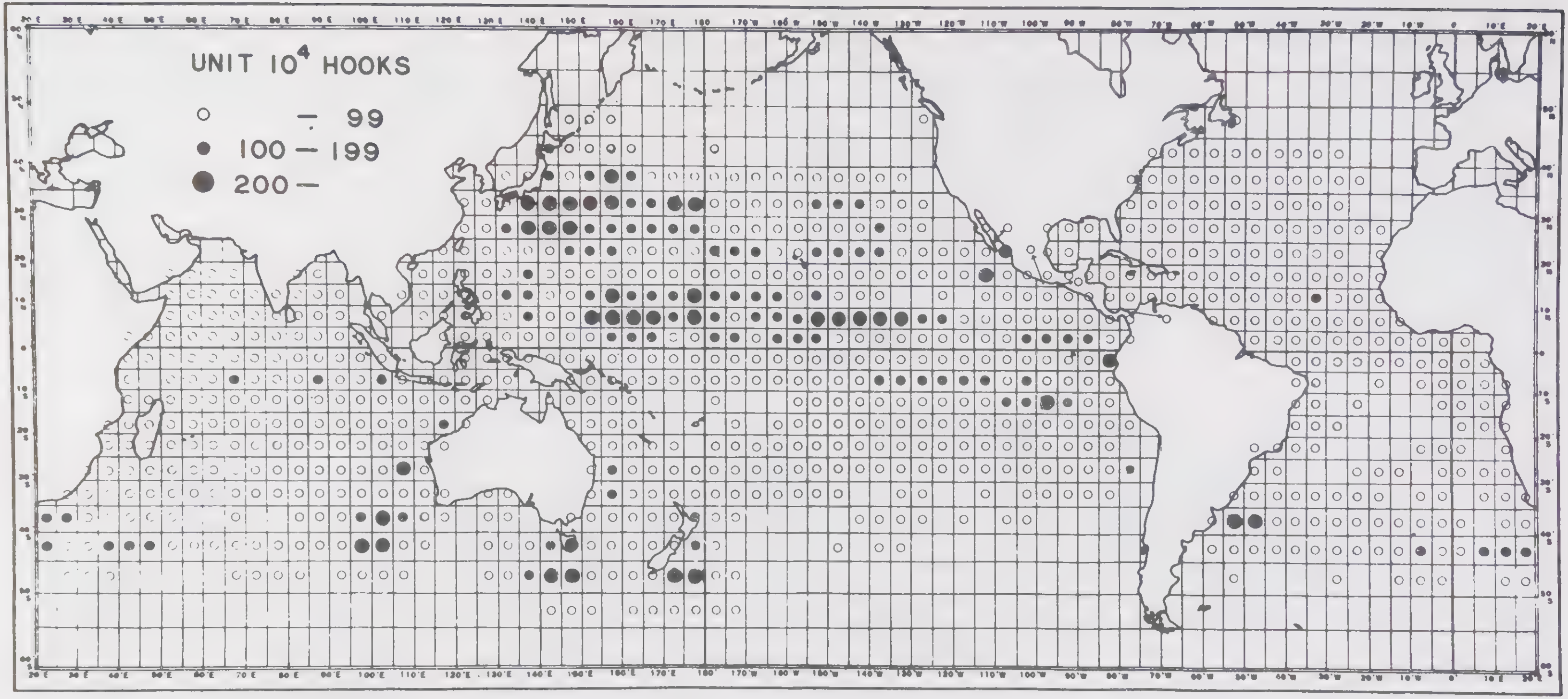

UNIT 10⁴ HOOKS
○ – 99
● 100 – 199
⬤ 200 –

Figure 8.—Distribution of estimated total fishing effort, in numbers of hooks per unit area (1970).

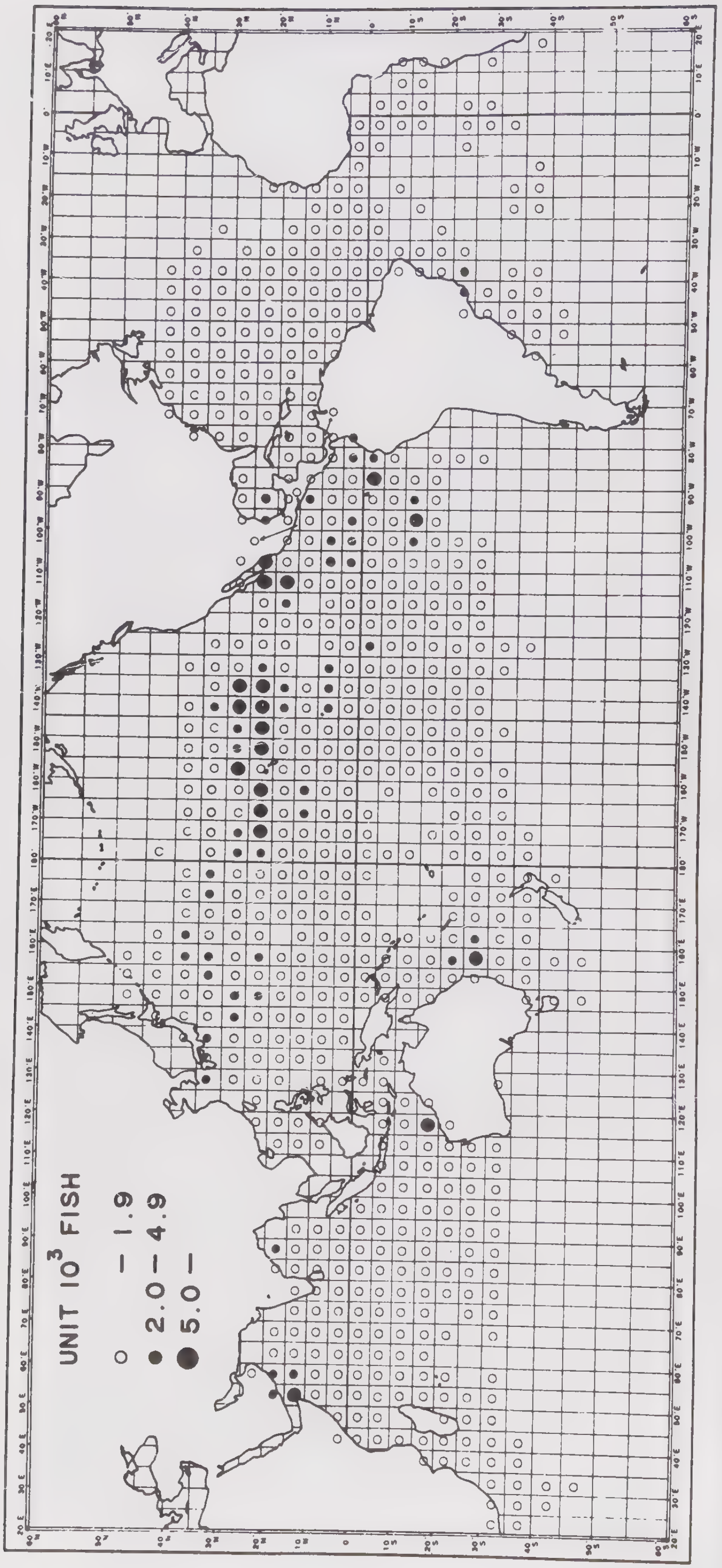

UNIT 10^3 FISH
○ — 1.9
● 2.0 — 4.9
● 5.0 —

Figure 9.—Distribution of the catch of striped marlin in numbers per unit area (1970). Catch data in Atlantic Ocean area pertains to white marlin, *Tetrapturus albidus*.

ndings. The Indian Ocean landings of striped marlin mount to approximately 20% of the Pacific landings.

aximum equilibrium yield: Honma and Suzuki 969) made some preliminary determinations of the aximum sustainable yield on the basis of 1960-66 ata. They suggested that striped marlin catches in e Pacific can probably be increased about 60% over e recent average annual landings.

However, judging by the fact that catches have veled off in recent years after fishing effort has vir-ually covered all of the known areas of striped marlin istribution, it appears that the present catches may e close to the maximum equilibrium yield level.

Obviously, further research is needed on this sub-ect.

PROTECTION AND MANAGEMENT

6.1 Regulatory (Legislative) Measures

6.11 Limitation on reduction of total catch

The Japanese tuna longline fishery is regulated in erms of fleet size by the vessel licensing system. icensing is reviewed at 5-yr intervals and fleet size is overned on the basis of the condition of the tuna esources. No increase in fleet size has been permitted ince 1963. However, other countries such as Korea and Taiwan have increased the size of their longline leet.

POND FISH CULTURE

Not applicable.

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SWIMMING ENERGETICS OF THE LARVAL ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

A modification of Gray and Hancock's theoretical method for studying propulsion of spermatozoa was used to estimate the energy expenditure of swimming anchovy, *Engraulis mordax*, larvae. Wave parameters obtained from photographs of feeding anchovy larvae were incorporated into a time dependent sinusoidal body displacement function which is used in the iterated energy integrals of the model. The integrals were numerically evaluated by 2-dimensional 16-point Gaussian-Legendre quadrature. The results for the mean larval length of 1.4 cm was 144.8 ergs/swimming excursion or 4.91×10^{-3} cal/h using known excursion rates. O_2 consumption measurement of similar size larvae indicate a 2.19×10^{-2} cal/h requirement. Extension to other larval sizes can be made using this model with certain qualifications. The relationships of swimming energetics to larval fish behavior are discussed. Current theories of large amplitude intermittent swimming are also discussed in light of the high swimming efficiencies encountered in this study.

The theoretical evaluation of swimming fish energetics by hydrodynamic analysis has been an extensively treated subject in recent years. Most of these treatments however have concentrated on calculation of thrust and thrust efficiencies with the exception of Lighthill (1970, 1971) who gave direct estimates for the mean swimming work rate and has drawn attention to the importance of the accelerative, virtual mass contributions in estimates of mean swimming work rate. Most expositions, however, deal with situations where inertial effects predominate with all subsequent derivations being consistent with that assumption (Taylor, 1952a). The low Reynolds number range of swimming energetics primarily of spermatozoa, has also been extensively treated (Taylor, 1951, 1952b; Gray and Hancock, 1955; Carlson, 1959; Holwill and Miles, 1971). All these treatments disregard inertial and accelerative effects in comparison with viscous effects in their treatment. Also, both viscous and inertial treatments calculate or estimate the mean swimming work rate after steady motion has been established.

The problem attacked in this paper is a synthesis and extension of the two classes of treatments discussed above, specifically to determine the energy expended per excursion by the 1-cm larval anchovy, *Engraulis mordax*. The term excursion as used here requires some elaboration. Larval anchovies have a peculiar swimming behavior because they do not continuously propagate caudally directed waves. In the adult form this behavior is noticeable by observing the tail, i.e., it does not beat continuously even though the fish appears to maintain constant forward motion. In the larval stages, however, this behavior results in an obvious discontinuous motion. The result is a series of bursts of motion from rest to rest which hereafter I refer to as excursions.

The estimation of excursion energetics by a theoretical model rather than indirect metabolic estimators during excursions is demanded because of the small size of the organisms considered, their discontinuous motion, and the investigator's inability to determine which fraction of the total energy consumption is due to swimming alone.

The parameters used in the model to calculate the excursion energy are taken from photographs of a larval anchovy of a specified size executing excursions in search of prey organisms. Since the search for prey constitutes a large proportion of the larva's activity, following Kerr (1971) we can write the total metabolism of the larva as,

$$T_T = T_F + T_C + T_S$$

where T_T = total metabolism
T_F = cost of search for prey

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T_S = standard metabolism
T_C = internal cost of food utilization.

The growth efficiency and subsequent relations derived from T_T are important in estimating fish yields in relation to standing food resources and other factors important to fisheries management. It is this larger view which gives relevance to the rather involved procedure of simply calculating one part of the value of T_T, namely T_F.

THEORY

The derivation of the excursion energy estimate is based on Gray and Hancock's (1955) development for spermatozoa. Instead of a cylinder with an inert head attached, the anchovy larva is regarded here as a ribbon or plate of specified width attached to an inert head (Figure 1). The assumption that the body is a ribbon is justified only if the ratio of the width to thickness (W/t) is $\gg 1$. In the larvae examined in this study this ratio averaged 2.5. While this ratio is not $\gg 1$ I have assumed that it is to simplify the problem. However, the error introduced is, I believe, minimal.

From Figure 1 the following relation is noted and will be used in the following derivations:

$$V_N = V_y \cos\theta - V_x \sin\theta \qquad (1)$$

$$V_T = V_y \sin\theta + V_x \cos\theta \qquad (2)$$

where V_N = normal velocity of an element of body
V_T = tangential component
V_y = y-component
V_x = x-component.

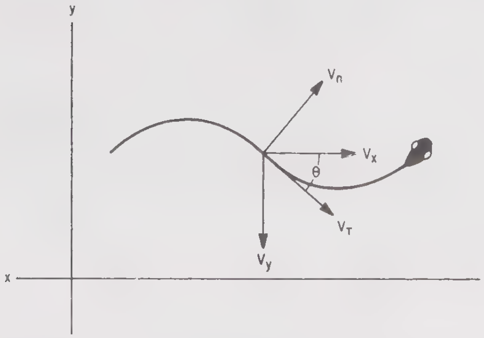

FIGURE 1.—Diagram illustrating the relationship of the velocity components of an element of body when moving transversely in the X-direction.

With the body approximated as an inextensible ribbon we find the use of the normal drag coefficient, C_N, and the tangential drag coefficient, C_T, convenient in addition to an appropriate sagittal contour function $h(s)$ where s denotes distance along the spine of the fish (see Figure 4).

The expression for the velocities V_N and V_T is first expressed in terms of the function which represents the propagated wave along the body $y(x,t)$, and V_x. By noting,

$$V_y = \frac{dy}{dt} \text{ and } \tan\theta = \frac{dy}{dx}$$

we can rewrite Equations (1) and (2) as,

$$\frac{V_N}{\cos\theta} = \frac{dy}{dt} - V_x \frac{dy}{dx} \text{ and } \frac{V_T}{\cos\theta} = \frac{dy}{dt}\frac{dy}{dx} + V_x .$$

$$\text{Given } \cos\theta = \frac{1}{[1+\tan^2\theta]^{1/2}} = \frac{1}{\left[1+\left(\frac{dy}{dx}\right)^2\right]^{1/2}}$$

$$\text{we get } V_N = \left[\frac{dy}{dx} - V_x \frac{dy}{dx}\right]\left[1+\left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (1')$$

$$V_T = \left[\frac{dy}{dt}\frac{dy}{dx} + V_x\right]\left[1+\left(\frac{dy}{dx}\right)^2\right]^{-1/2} \qquad (2')$$

Now we may proceed to write the contributions to the total work of excursion made by the head, body viscous reactive terms, and accelerative body virtual mass.

The element of work performed in moving the inert head is given by,

$$dW_H = 1/2\,\rho\, C_H\, A\, V_x^3\, dt + (m+M)\frac{dV_x}{dt} V_x\, dt$$

(Vlymen, 1970)

where dW_H = element of work performed by the head
C_H = drag coefficient of the head
A = cross-sectional area
m = virtual mass of head
M = mass of head
ρ = density of seawater.

Thus, given the time of excursion as t_E we get,

$$W_H = 1/2 \int_0^{t_E} (\rho\, C_H A\, V_x^3 + 2(m+M) \frac{dV_x}{dt} V_x)dt. \qquad (3)$$

The element of work performed by the body contributed by viscous-reactive forces can be approximated using experimental values for the normal and tangential drag coefficient of a smooth plate. The choices made are

$$C_N = \frac{k_N}{Re} = \frac{20.37}{Re} \quad \text{(Hoerner, 1965)} \qquad (4)$$

$$\text{and } C_T = \frac{k_T}{\sqrt{Re}} = \frac{1.328}{\sqrt{Re}} \quad \text{(Schlicting, 1960)} \qquad (5)$$

where Re is the appropriate Reynolds number respectively. Although these are primarily low Reynolds number approximations they are within 10% at $Re = 30$. Thus F_N, the normal force on a plate of frontal area A is given by

$$F_N = 1/2\, \rho\, C_N V_N^2\, A.$$

Since for any position along the fish body

$$Re = \frac{2V_N h(s)}{\nu}$$

ν the kinematic viscosity, we get using C_N from Equation (4) the normal force dF_N on an element of body ribbon as,

$$dF_N = \frac{\rho k_N \nu}{4 V_N h(s)} V_N^2\, 2h(s)\, ds = \frac{\rho}{2} k_N\, \nu\, V_N\, ds.$$

In a similar manner F_T, the tangential force on a plate of total wetted surface area A, is

$$F_T = 1/2\, \rho\, C_T V_T^2\, A.$$

Since the formula for C_T above uses $Re = \frac{V_T l}{\nu}$ where l is distance measured along the body, we get the tangential force dF_T on an element of body ribbon as

$$dF_T = \frac{2\rho k_T \sqrt{\nu}}{\sqrt{V_T s}} V_T^2\, h(s)\, ds$$

$$= 2\rho k_T \sqrt{\nu}\, V_T^{3/2} \frac{h(s)}{\sqrt{s}} ds. \qquad (7)$$

Multiplying each element of force above by the element of distance in the direction of that force and summing yields,

$$dW_B^{V.R.} = \frac{\rho}{2} k_N\, \nu\, V_N^2\, dsdt + 2\rho\, k_T \sqrt{\frac{\nu}{s}}\, V_T^{5/2}\, h(s)\, dsdt$$

where $dW_B^{V.R.}$ is the element of viscous reactive work performed by an element of body ribbon. Using the Equations (1′) and (2′) for V_N and V_T and integrating over the excursion time t_E and projected body length excluding the head we get,

$$W_B^{V\,R} = \frac{\rho}{2} \int_0^{t_E} \int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx} \right]^2}{\left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{1/2}} \right] dsdt$$

$$+ \rho \int_0^{t_E} \int_{l_H}^{l} \frac{2 k_T \sqrt{\nu} \left[\frac{dy}{dt} \frac{dy}{dx} + V_x \right]^{5/2} h(s)}{\sqrt{s} \left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{3/4}} dsdt.$$

where l_H is the x-projected length of the inert head. Eliminating ds by the relation,

$$ds = \left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{1/2} dx$$

yields finally,

$$W_B^{V.R.} = \frac{\rho}{2} \int_0^{t_E} \int_{l_H}^{l} \left[\frac{k_N \nu \left[\frac{dy}{dt} - V_x \frac{dy}{dx} \right]^2}{\left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{1/2}} \right] dxdt$$

$$+ \rho \int_0^{t_E} \int_{l_H}^{l} \frac{2 k_T \sqrt{\nu} \left[\frac{dy}{dt} \frac{dy}{dx} + V_x \right]^{5/2} h(s)}{\sqrt{s} \left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{3/4}} dxdt.$$

As will be noted s is present in the second of the integrals above; however, later in the discussion s and $h(s)$ will be converted to appropriate functions of x and t so that the integrations may be performed.

The accelerative or virtual mass element of work can be calculated using the fact that the virtual mass of a flat plate accelerating parallel to its normal vector is equal to the mass of the fluid enclosed in a circumscribing cylinder having the plate chord as diameter (Fung, 1969). Hence from Figure 2 the virtual mass is given by

$$dM = \rho \pi h^2(s)\, ds$$

and the magnitude of the acceleration by

$$a \sin \theta_1 = a \sin(\theta - \theta_2)$$

where $a = \left| \tilde{a} \right|$.

Now $\theta = \tan^{-1} \dfrac{dy}{dx}$ and $\theta_2 = \tan^{-1} \dfrac{V'y}{V'x}$

where $V'y = \dfrac{dVy}{dt}$ and $V'x = \dfrac{dVx}{dt}$, giving

$$a \sin(\theta - \theta_2) = a \sin \left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x} \right)$$

Since $\left| \tilde{a} \right| = \left(V'^2_y + V'^2_x \right)^{1/2}$, we get

$$a \sin(\theta - \theta_2) = \left(V'^2_y + V'^2_x \right)^{1/2} \cdot \sin \left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x} \right)$$

Thus the magnitude of force $F_{V.M.}$ on an element of body ribbon due to induced mass dM is

$$\left| F_{V.M.} \right| = a\,dM = \rho \pi h^2(s) (V'^2_y + V'^2_x)^{1/2} \cdot \sin(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x}).$$

Since the element of work is given by

$$dW = \left| F_{V.M.} \right| \cdot \left| dx \right| \cdot \cos(F_{V.M.} \,|\, dx)$$

where

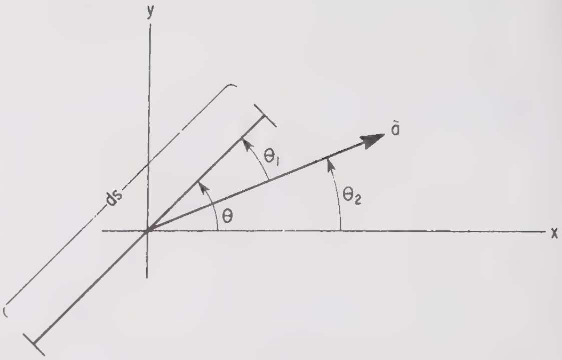

FIGURE 2.—Diagram illustrating body element undergoing acceleration $\tilde{a}$ and relationships of orientation of element to vector $\tilde{a}$ in terms of the angles θ, θ_1, θ_2.

$$\left| dx \right| = (V_y^2 + V_x^2)^{1/2}\, dt$$

and

$$\cos(F_{V.M.} \,|\, dx) = \cos(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx}),$$

we get finally

$$dW = \rho \pi h^2 (s) (V_y^2 + V_x^2)^{1/2} \quad (V'^2_y + V'^2_x)^{1/2} \cdot \sin \left(\tan^{-1} \frac{dy}{dx} - \tan^{-1} \frac{V'y}{V'x} \right) \cdot \cos \left(\tan^{-1} \frac{V'y}{V'x} - \tan^{-1} \frac{Vy}{Vx} \right) dsdt.$$

Using the identities for cos $(a - b)$, sin $(a - b)$, and ds gives finally,

$$dW^A_{B_\text{I}} = \frac{\rho \pi h^2(s) \left[\frac{dy}{dx} V'x - V'y \right] \left[V'x \; Vx + \frac{dy}{dt} \frac{d^2y}{dt^2} \right] dxdt}{\left[V'^2_x + \left(\frac{d^2y}{dt^2} \right)^2 \right]^{1/2}}$$

where $dW^A_{B_\text{I}}$ is part I of the element of work performed by the acceleration of the surrounding fluid.

In addition to $dW^A_{B_\text{I}}$ above we also want the work done in accelerating the body itself. Calling $\rho_B(s)$ the linear mass density of the body we get, using Figure 2,

$$dW^A_{B_{II}} = \rho_B(s)\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} \cdot \left(V^2_x + V^2_y\right)^{1/2} \cdot \cos\left(\tan^{-1}\frac{V'y}{V'x} - \tan^{-1}\frac{Vy}{Vx}\right) dsdt$$

where $\left(V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right)^{1/2} = \left|a\right|$,

$\left(V^2_x + V^2_y\right)^{1/2}\ dt = \left|dx\right|$,

$\rho_B(s)\ ds = dm.$

When the above terms are expanded we get, taking account of *ds*,

$$dW^A_{B_{II}} = \rho_B(s)\left(Vx\, V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right) \left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dxdt.$$

Integrating $dW^A_{B_I} + dW^A_{B_{II}}$ from 0 to t_E in t and l_H to l in x we get the accelerative body work,

$$W^A_B = \int_0^{t_E}\int_{l_H}^{l} \rho_B(s)\left(Vx\ V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right)\left(1 + \left(\frac{dy}{dx}\right)^2\right)^{1/2} dsdt \qquad (8)$$

$$+\ \rho\int_0^{t_E}\int_{l_H}^{l} \pi h^2(s)\frac{\left[\frac{dy}{dx}V'x - V'y\right]\left[Vx\ V'x + \frac{dy}{dt}\frac{d^2y}{dt^2}\right]}{\left[V'^2_x + \left(\frac{d^2y}{dt^2}\right)^2\right]^{1/2}}\ dxdt.$$

The total work estimated per excursion is then given by the sum of W^A_B, $W^{V.R.}_B$, and W_H.

METHODS

Motion picture photographs (16 mm, 128 fps) of swimming and feeding anchovy larvae were used to ascertain the various parameters in the proposed body displacement function $y(x, t) = A\ (t) \sin\frac{2\pi}{\lambda(t)}\left(x + \frac{dx_w}{dt}t\right)$ where $A\,(t)$ is the wave amplitude of the propagated wave, $\lambda(t)$ the wavelength and $x_w(t)$ the wave position as functions of time. Because of the intermittent character of the motion, variance with x was not considered as important an independent variable as t in the various functions comprising $y\ (x, t)$. The above displacement function is a general time dependent analogue of the function chosen in Holwill and Miles (1971).

The motion pictures used were obtained from John Hunter of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, and the techniques used in obtaining them are described fully (Hunter, 1972). The particular sequences used were of fish larvae varying in length from 1.2 to 1.7 cm standard length. All sequences were analyzed starting with the larvae at rest through the sine-wave execution and subsequent forward movement to rest again. The x-axis was considered to be parallel to the direction of forward motion as monitored by a point midway between the eyes of the fish. This point was also used to monitor forward progression.

The sequences were projected with a 16-mm Kodak[2] analyst projector on an elevated stand, through a right-angle mirror onto a table enclosed with a darkened viewing hood. At the beginning of an excursion the contour of the body was outlined with a fine-point pen on heavy-duty, low-absorbance paper. Once the outline was traced, the next frame was advanced (each frame representing 1/128 of a second) until the larva came to rest again. The mean excursion time of the larvae examined was 12.9 frames. The contour sequences thus obtained were taken to be representative of the feeding-searching behavior and were used in elucidating the wave-form parameters. In addition to the wave-contour parameters, the midpoint between the eyes was monitored for use in determining Vx and $V'x$.

When the above contours and position points were obtained along with the proper magnification factors derived from knowledge of the lengths of the fish in a particular film, relevant parameter values from the tracings were directly measured using a set of dial calipers read to 0.01 cm.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Many of the initial sequences of an excursion when viewed with respect to the x-axis as defined above showed the appearance of a wave along the proximal portion of the fish while the rest of the body coincided closely to the x-axis. This indicated strong x-dependence of the amplitude in the initial portion of the excursion. However, after three frames an almost symmetrical amplitude wave was observed. Thus the amplitude in the first several frames was taken as the maximum length of the wave above the x-axis (Figure 3).

The wave length was taken as that length between two successive crossings of the x-axis by the displacement wave form. During the later part of the excursions no crossings from positive to negative were observed and at this point the wavelength was taken as twice the value from one tangent of the body on the line of motion to the other (Figure 3).

The position of the midpoint between the eyes after each frame was monitored to yield $x(t)$. Each successive movement of that reference point was recorded in the manner outlined above and the distance moved during each frame noted.

The projected length $x_P(t)$ was taken as the length between the two points representing the projection of the tail and snout tip position on the x-axis and was used in a manner to be described later.

The wave position $x_w(t)$ was taken as the projected length of the body from the point where $A(t)$ is measured to the snout tip (Figure 3).

The points representing the functions described above at each unit of time, i.e., one frame, were collected for 18 excursions which were randomly selected from the larval anchovy feeding films. The functions were then nondimensionalized by division by body length and plotted. The geometric form of the resulting function was then used as a guide in selecting an appropriate descriptive function. The parameters of these functional forms were then fitted by computer in the least squares sense using a nonlinear steepest descent approach (Conway, Glass, Wilcox, 1970). The graphical representation of the proposed body displacement function with the internal functions fitted in this manner was found to coincide very closely with the actual body displacements seen in the films.

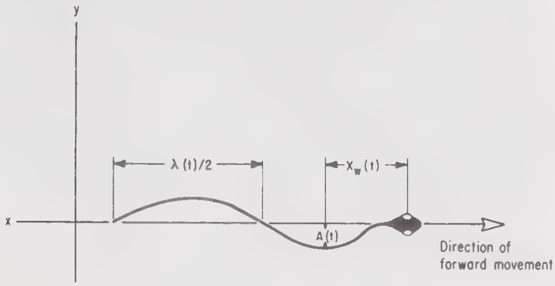

FIGURE 3.—Diagram illustrating the identification of (t)/2, $X_w(t)$ and $A(t)$ from photographic records (see text).

In the derivations for total excursion work, W_T, the integral for tangential viscous reactive work contains s, the distance along the fish body, explicitly. The function satisfying $F(x, t) = s$ is extremely complicated for the complete wave-form displacement function using all the fitted internal functions and is almost impossible to calculate explicitly. The alternative used here is to extrapolate back from the measured $x_p(t)$ to yield $s\ (x, t)$.

We know the function $F(x, t) = s$ satisfies

$$F(x_p, t) = L$$

where L is the length of the fish body. Since the maximum amplitude ever encountered in this study was around 0.2 L and the mean integration distance never greater than $\pi/2$, we can calculate, for purposes of comparison, the differences between the true length of a pure sine wave of amplitude A and its projected length.

The unperturbed or no sine-wave form for a $\pi/2$ interval of integration yields simply $\pi/2$. The sine-wave projected length is, for $y = A \sin\theta$,

$$s = \int_0^{\pi/2} \sqrt{1 + A^2 \cos^2 \theta}\, d\theta$$

$$= \sqrt{1 + A^2}\ E\left(\pi/2, \frac{A}{\sqrt{1 + A^2}}\right)$$

where $E(\Phi\ , k)$ is the elliptic integral of the second kind (in this case a complete elliptic integral of the second kind). Taking $\lambda \approx 2.0$ cm we get using $A = 0.2L$.

$$s = \sqrt{1 + 0.16}\ \ E(\pi/2, 0.37) = 1.625.$$

The difference between this and $\pi/2$ is about 4%. Thus, we expect the projected length and real body length to differ only slightly. With this confidence we make the following additional assumptions:

$$F(\lambda x_p, t) = \lambda L. \qquad \lambda \leq 1$$

This assumption based on the error calculation above postulates a linear relation between projected length and real length. Now $x_p/L = x_p(t)$ and is obtained from excursion analyses. We can rewrite this as

$$\frac{x_p}{x_p(t)} = L$$

$$\frac{\lambda x_p}{x_p(t)} = \lambda L \qquad \lambda \leq 1$$

$$\frac{x}{x_p(t)} = s \qquad x \leq x_p$$

Thus we chose to identify

$$F(x, t) = x/x_p(t) = s(x, t).$$

The determination of the contour $h(s)$ was made using biologically accurate drawings of a 1.84-cm anchovy larva. The term $h(s)$ was established for the body distal to a vertical line tangent to the gill plate as shown in Figure 4. From that point to the beginning of the tail $h(s)$ was taken as a constant and the relation $h(s) = 0.038\,L$ was found to hold. The dorsal and anal fin contributions were neglected because the plate approximation already constitutes an upper bound estimate for W_T. Thus, the neglect of these fins quantitatively yields a more realistic estimate of W_T. Using the notation of Figure 4 we have,

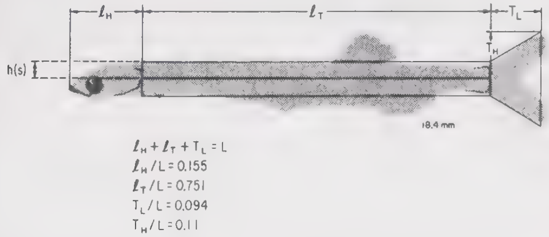

FIGURE 4.—Lateral cross section of 1.84-cm anchovy larvae displaying relationship of idealized contour function $h(s)$ (see text) to appropriate nondimensionalized morphometric parameters.

$$h(s) = 0 \text{ for } s \leq l_H$$

$$h(s) = 0.038\,L \text{ for } l_H < s \leq (l_H + l_T)$$

$$h(s) = 0.038\,L + \frac{(T_H - 0.038\,L)}{T_L}\,[s - (l_H + l_T)]$$

$$\text{for } (l_H + l_T) < s \leq L$$

or using values in Figure 4 the last relation may be written

$$h(s) = 0.038L + 0.766\,(s - 0.906L).$$

The cross-sectional area A_H which appears in the work integral for the head was determined by randomly selecting Formalin-preserved anchovy larvae from 0.5 to 1.5 cm in length and affixing them, via the Formalin surface tension on their bodies, upright on the side of a small inverted beaker. The largest cross section of the head was then viewed directly with a Nikon optical comparator and an outline traced from the lighted viewing screen. Lengths of the bodies were also measured with dial calipers at the time the tracings were made. Subsequently the tracing areas were measured with a planimeter and corrected to the true value. A least squares analysis of the results yielded the relation $A_H = 0.00423L^{1.23}$ where L is in centimeters and A_H is in square centimeters. The graph is plotted along with the data in Figure 5.

The representation for $\rho(s)$, the linear density of the body, was regarded as constant for any given length and calculated from data in Lasker, et al., (1970). Assuming 90% water, the wet weight of 0.5- to 1.6-cm larvae is then given by $0.00319L^{2.3237} = \rho(s)$ where L is in centimeters and $\rho(s)$ is in grams per centimeter.

The density of the seawater was taken for $T = 17°\text{C}$ and was 1.02454. This value was obtained from tables published by the U.S. Navy Hydrographic Office (1956).

In my formulation I assume that the head is propelled through the water as an inert object attached to an undulating body. We want to know the virtual mass and drag coefficient of the inert head for use in the W_H integral. Since the shape of the anchovy larva's head is

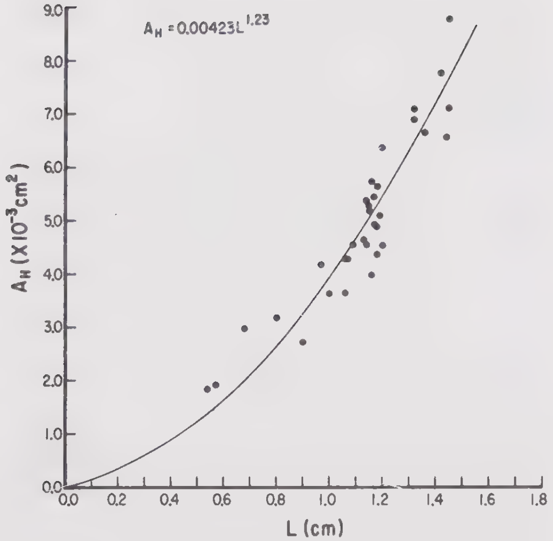

FIGURE 5.—Cross sectional area of larval anchovy head, A_H, as a function of length L.

roughly ellipsoidal or a bluff body, I decided to modify, with due consideration for the geometric differences, the drag relationship observed for a copepod (*Labidocera trispinosa*), which is a naturally occurring bluff body of similar shape, to represent the relevant characteristics of the anchovy larvae head.

If the copepod is taken as an equivalent ellipsoid, we get, from data in Vlymen (1970),

$$\overline{\left(\frac{a_c}{b_c}\right)} = 2.9$$

where a_c is the major axis length and b_c is the semimajor axis length of the copepod *L. trispinosa* and is given respectively by $a_c = \frac{L_c}{2}$ (one-half the metasome length) and $b_c = \left(\frac{A_H}{\pi}\right)^{1/2}$. For the anchovies studied $\frac{l_H}{L} = 0.155$ (Figure 4) and for $\bar{L} = \underline{1.4 \text{ cm}}$ and $A_H = 0.007$ cm², $l_H = 0.217$ cm yielding $\overline{\left(\frac{a_a}{b_a}\right)} = 2.3$.

For high Reynolds numbers ($\sim 10^4 - 10^5$) and rotationally symmetrical bluff bodies of various l/d ratios, where l is the bluff body length and d is diameter, we have

$$\frac{C_{D\cdot}}{C_f} = 3\left(\frac{l}{d}\right) + 4.5\left(\frac{d}{l}\right)^{1/2} + 21\left(\frac{d}{l}\right)^2$$

(Hoerner, 1965)

where C_f is the frictional drag coefficient based on wetted surface area and $C_{D\cdot}$ is the drag coefficient based on frontal area. We can use this relation to approximate $\frac{C_{D\cdot}\ (\overline{l}/d = 2.9)}{C_{D\cdot}\ (\overline{l}/d = 2.3)}$ assuming $C_f(l/d = 2.9) \cong C_f(l/d = 2.3)$, and use the above ratio to modify the measured drag relation already obtained for the copepod. Substituting $l/d = 2.9$ and $l/d = 2.3$ into the relation for $C_{D\cdot}/C_f$ we get on dividing

$$\frac{C_{D\cdot}\ (l/d = 2.9)}{C_{D\cdot}\ (l/d = 2.3)} = 1.00.$$

At lower Reynolds numbers we expect the geometric differences to cause a greater discrepancy between $C_{D\cdot}$ $(l/d = 2.9)$ and $C_{D\cdot}$ $(l/d = 2.3)$. In particular $C_{D\cdot}$ $(l/d = 2.9) > C_{D\cdot}(l/d = 2.3)$. However, since in my experiments *Re* was from 0- to 100, the region where we expect the C_D (*Re*) curve to flatten out to a fairly constant value we take C_D (*Re*) for the copepod as a first approximation to the $C_{D\cdot}$ (*Re*) for the anchovy head. That function is $C_D\ (Re) = 85.2/Re^{.80}$, Vlymen (1970). The virtual mass, m, occurring in the integrals for W_H is then calculated by considering the head as if it were an equivalent ellipsoid. Using $(a_a/b_a) = 2.3$ we can calculate

m as $m = k_1 \rho V_D$ where $k_1 = \frac{\gamma}{(2-\gamma)}$

$$\gamma = 2\left(\frac{1-\epsilon^2}{\epsilon^3}\right)\left[1/2 \log\left(\frac{1+\epsilon}{1-\epsilon}\right) - \epsilon\right]$$

$$\epsilon = \left(1 - \frac{b_a^2}{a_a^2}\right)^{1/2}$$

$V_D = 4/3\pi a_a b_a^2$ Vlymen (1970).

For a 1.4-cm larva m has a value of 1.80×10^{-4} g and assuming the head density is the same as seawater we get $M = 7.9 \times 10^{-4}$ g. Thus W_H may be rewritten as

$$W_H = 1/2 \int_0^{t_E} 85.2\left(\frac{\nu}{L}\right)^{.80} V_x^{2.2} A_H dt$$

$$+ \int_0^{t_E} (9.7 \times 10^{-4} \frac{dV_x}{dt} V_x\, dt$$

where ν is the kinematic viscosity of seawater 0.0119 cm^2–s^{-1} (U.S. Navy Hydrographic Office, 1956).

A computer program by Stroud (1971) using 16-point Gauss-Legendre integration, and the above outlined integration scheme was used to compute the integrals comprising W_T. The program was translated into Algol and executed on a Burroughs 6700 at the University of California, San Diego Computer Center. Accuracy of the program was checked by evaluation of the iterated integrals

$$\int_0^w e^{-y^2}\,dy \int_0^y e^{x^2}\,dx \text{ for various } w \text{ and}$$

$$\int_0^1 \int^{\sqrt{1-x^2}} \sqrt{1-x^2-y^2}\;dy\,dx = \frac{\pi}{6}.$$

The results showed the integration scheme to be accurate to the eighth decimal place in the former integral when compared with tables in Rosser (1948) and accurate to the fourth decimal place in the latter integral using standard tables. Details of the mathematical scheme are found in the appendix.

In the integrations of W_T a relative convergence was computed by first doing the integration over the whole interval, that is,

$$I_0 = \int_0^t \int_{f(t)}^{g(t)} F(x,\,t)\;dxdt.$$

Then the value corresponding to one subdivision is computed, namely,

$$I_1 = \int_0^{t/2} \int_{f(t)}^{g(t)} F(x,\,t)\;dxdt$$

$$+ \int_{t/2}^{t} \int_{f(t)}^{g(t)} F(x,\,t)\;dxdt.$$

The relative convergence is then computed as

$$C = \frac{I_1 - I_0}{I_1}.$$

If this value is less than 0.05, the value I_2 is taken as the value of the integral. If it is greater, the intervals comprising I_2 are further subdivided and the process continued until convergence is reached. Thus, if I_n, corresponding to 2^n subdivisions, and I_{n+1}, corresponding to 2_{n+1} subdivisions, are of such values that

$$\frac{I_{n+1} - I_n}{I_{n+2}} < 0.05,$$

then I_0 is assigned the value I_{n+1}.

The convergence is set higher than one might expect because computation of the complex integrals of the type used in this study is manifested by slow and oscillatory relative convergences necessitating a great deal of computer time. However, when the convergence criteria was set at 0.05 in the integrations performed, convergences were better than the critical value. The effect of the higher convergence criteria is thus seen as being an economic and computational convenience.

RESULTS

The plotted values of the nondimensional amplitude, $A(t)/L$, wave position, $X_w(t)/L$, and projected length, $X_p(t)/L$, along with the descriptive functions fitted by the methods discussed are shown in Figures 6 and 7. The points comprising the curves of each represent the mean value of the particular parameter in question at successive units of time where one time unit is $^1/_{128}$ s.

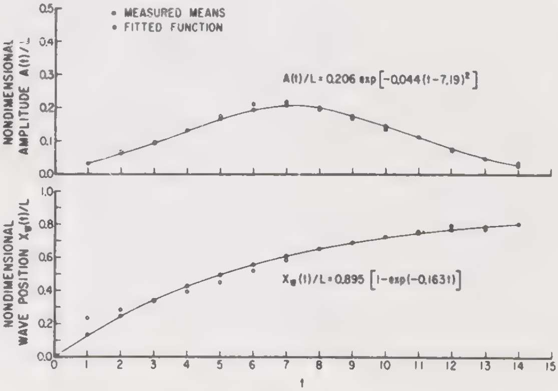

FIGURE 6.—Nondimensional amplitude, $A(t)/L$ and wave position, $X_w\ (t)/L$, of body displacement function as functions of time, t, in motion frame units. The graphs display the fitted curves (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

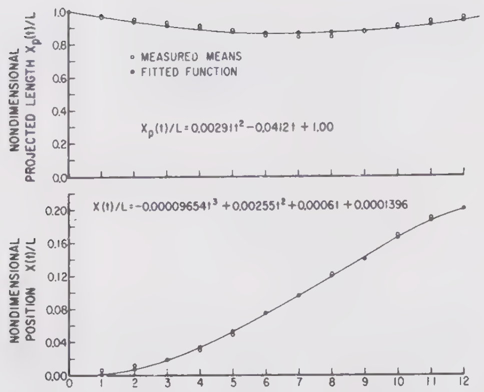

FIGURE 7.—Nondimensional position, $X(t)/L$, and projected body length, $X_p(t)/L$, as functions of time, t, in motion frame units. The graphs display the fitted curves (lines) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles).

The curve for $\lambda(t)/L$, deserves some discussion. Since the amplitude of the propagated wave was known to be zero at $t = 0$, both $\lambda = \infty$ or $\lambda = 0$ would be descriptive of the initial straight-line configuration. However, $\lambda = 0$ implies an infinite number of oscillations varying like sin t/λ with neither the function nor the first derivative existing as $\lambda \rightarrow 0$. Since at the end points of an excursion a slightly perturbed wave form was observed, i.e., a finite wavelength, the nondimensional wavelength of the $t = 0$ excursion wave form was adjusted to be equal to the last. A perfect relation would have $\lambda = \infty$ at both end points. This, I believe, does not drastically affect the results since the only modulatory component at the end points is the amplitude which is zero at these points. This accounts for the Lennard-Jones type of function which was chosen as a functional representation of $\lambda(t)/L$ and is shown in Figure 8 along with the function itself. The values at other than the end points together with the fact that $A(t) = 0$ at these points is sufficiently descriptive of the contour wavelength to vitiate any physical inconsistencies or mathematical problems that may arise from the end point modification of $\lambda(t)/L$ discussed.

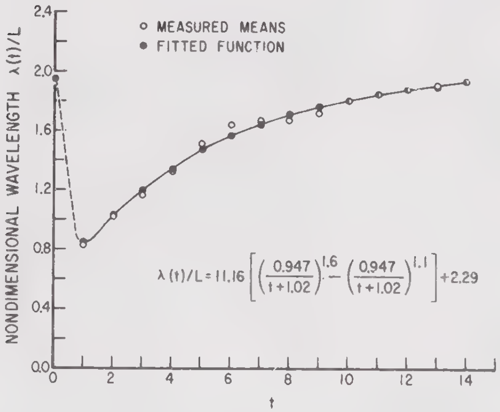

FIGURE 8.—Nondimensional wavelength, $\lambda(t)/L$, as a function of time, t, in motion frame units. The graph displays the fitted function (line) together with the original data (open circles) and points of the fitted curve at corresponding time units (closed circles). The dotted portion of the fitted curve is discussed in the text.

The integrals representing the work per excursion namely $W_B^{V.R.}$, W_B^A, W_H were subdivided further into smaller iterated integrals and, using the mean excursion time of 12.9 frame time units (~0.10s) integrated by the method already outlined. The values obtained were taken to represent the work/excursion of an anchovy larvae of length equal to the mean of the animals used in the study or 1.4 cm.

The values of the work are divided into five categories as follows: 1) head energy representing the value of the integral in Equation (3), 2) normal energy representing the value of the 1st integral of $W_B^{V.R.}$, 3) tangential energy representing 2nd integral of $W_B^{V.R.}$, 4) body inertial energy representing the 1st integral of W_B^A, and 5) inertial energy representing the 2nd integral of W_B^A. The value of these five integrals in ergs/excursion and their fraction of the total excursion energy is given in Table 1. It is observed from the table that accelerative terms such as body inertial and inertial energies account for more than three-fourths of all the energy used in swimming. It is worthwhile noting that although this is an expected outcome of the peculiar behavior of the anchovy larvae, it is possibly true that neglect of such terms in many analyses of fish energetics is cause for errors. Attention to these matters has been given thorough theoretical discussion in Lighthill (1970, 1971). The analysis in this paper,

TABLE 1.—Excursion energy components in ergs for the 1.4-cm anchovy larva.

Item	Energy/ excursion	Percent of total
Normal energy	11.5	7.9
Tangential energy	0.35	0.2
Inertial energy	33.6	23.2
Body inertial energy	99.2	68.5
Head energy	0.15	0.2
Total energy	144.8	

however, depends on incorporating what actually occurs into an easily manipulated theoretical energy construct.

Although the point of this study is to evaluate the swimming energetics in an indirect but nonmanometric manner, it is nevertheless interesting to compare the calculated energy using the theoretical model with values obtained using O_2 consumption measurements obtained with anchovy larvae. Such experiments in limited numbers have been performed by Lasker (pers. commun.) using more than one larva per experiment and with the animals confined to small volume containers. No knowledge of activity levels was possible during these experiments and the values obtained reflect total O_2 uptake per experimental period averaged for the number of larvae per container. Lasker believes, however, that activity levels during such experiments are below natural levels because of the inhibiting effects of the container surfaces and crowding. The value obtained from such experiments was $4.36 \pm 1.05\ \mu l\ O_2$/mg dry wt/h. Assuming an RQ of 0.70 we get 1 $\mu l\ O_2 = 0.005$ cal ± 0.00035 (Lasker, 1962). Thus, the caloric equivalent of the anchovy larval respiratory rate is between 0.0153 cal/mg dry wt/h and 0.0289 cal/mg dry wt/h with a mean value of 0.0218 cal/mg/h ($n = 23$). A comparison between the theoretically determined energy value and the mean O_2 uptake value given above requires a simultaneous knowledge of swimming activity expressed as an excursion frequency. Such information is not available and it is precisely our inability to make simultaneous observations of O_2 consumption and activity of fish larvae that necessitates the type of study undertaken in this paper. Excursion rates observed during 5-min feeding-searching periods have been measured (Hunter, 1972) using large containers. For the periods observed the excursion rate appropriate to a 1.4-cm larvae was found to be 1.57 ± 0.03 excursions/s with the mean time devoted to intermittent swimming being 82.6% ± 1.2%. This value is probably a maximum for activity since satiation would probably lead to a decrease in excursions as would the lack of observable food particles. Since available O_2 measurements were not collected during feeding, some modification of the above activity value has to be made to compensate for the inhibition of the container and the absence of food before these values can be used for comparison.

The O_2 consumption measurements of anchovy larvae were performed in small 70-ml containers in light and darkness. The only relative activity measurements that have been performed for similar situations were on 28-day-old herring larvae ca. 1 cm in length in a variety of light conditions by Blaxter (1973). Although herring are continuous swimmers, unlike anchovy larvae, the use of relative activities was deemed an appropriate way of estimating the activity variation of a similar sized nonfeeding organism in the following manner. For herring larvae at 10 different light levels the mean percent difference between maximum and mimimum activity levels was found by Blaxter (1973) to be 78.6%, maximum activity being defined as mean activity plus two standard errors and minimum activity as mean activity minus two standard errors. Although this change is large, it probably reflects behavioral modulation more than effects of the container since in Blaxter's experiment the container (a long tube) contained approximately 1,500 ml of seawater. Thus, regarding the O_2 consumption experiments on the anchovy as representing the minimum activity levels of that organism in the same relationship of active to inactive as found from Blaxter (1973), we can, using known maximum excursion rates during feeding from Hunter (1972), calculate the minimum excursion rate or activity corresponding to our O_2 measurements and hence the energy consumption for swimming based on that excursion rate. This analysis assumes the geometric swimming behavior during feeding and nonfeeding is the same, an assumption confirmed by observation.

Using the mean O_2 consumption value 0.0218 cal/mg dry wt/h and the dry weight of a 1.4-cm larva from Lasker et al. (1970) we get an expenditure of 22.6×10^{-3} cal/h. Taking 1.57 excursions/s as the mean maximum activity value, decreased by 78.6% to convert to minimum activity levels, and multiplied by the theoretically determined energy per excursion of the 1.4-cm larva of 144.8 ergs/excursion, we get 4.91×10^{-3} cal/h. This value yields an estimate of metabolic swimming efficiency of 24.6% for the 1.4-cm larval anchovy assuming a poikilothermic basal metabolic rate of 0.05 $\mu l\ O_2$/mg wet wt/h. This efficiency is quite high when compared to values obtained for larger fish where efficiencies in the range of 8 to 15% (Webb, 1971) are observed. However, such experiments are usually done on large fish constrained by relatively small tanks, swimming continuously, and using a caudal propeller mode of propulsion. Thus any comparison of the above results with the wide-range Reynolds number motions and large amplitude wave forms encountered in this study must be done cautiously and with appropriate consideration of hydrodynamical dissimilarities. However, using the most obvious behavioral differences between the two types of studies, a higher overall efficiency might be suspected based on the viewpoint of Lighthill (1971) that the large amplitude tail motions exhibited by some fishes be interpreted as a means of producing reactive thrusts which balance the enhanced viscous drag produced upon the commencement of lateral movements. Lighthill thus implies that large amplitude movements interspersed with periods of gliding are more efficient than continuous small amplitude oscillations as a mode of propulsion. This appears to be confirmed in the results of this study where the behavior is of this type and the efficiency apparently high. It should be stressed that a range of efficiencies can exist due to the intrinsic variability in O_2 consumption values and associated activity measurements and the fact that synchronous determinations of both have not yet been performed. The purpose of the swimming efficiency calculation and the associated comparison curves with O_2 values (Figure 9) is to demonstrate the relationship the theoretical values determined here have to the available physiological parameters obtained with simple experimental designs. If excursion energies could be obtained by simpler means, one could circumvent the involved procedures presented in this paper.

It is interesting to note that the Pacific sardine, *Sardinops caerulea,* whose ecological niche was primarily taken over by the anchovy, *Engraulis mordax,* in the California Current (Murphy, 1966) does not exhibit, in the larval stages, the same swimming behavior as the anchovy, i.e., swimming bursts followed by glides. Instead it swims by constant, small amplitude oscillating movements of the body. In light of the results here and theoretical work by Lighthill it is possible that the propulsive efficiencies in the larval stages of the sardine and anchovy are slightly different, the sardine being less efficient. Thus a small behavioral-propulsive difference between the anchovy and the sardine might have permitted the anchovy to compete more favorably when there was a decline in sardine population.

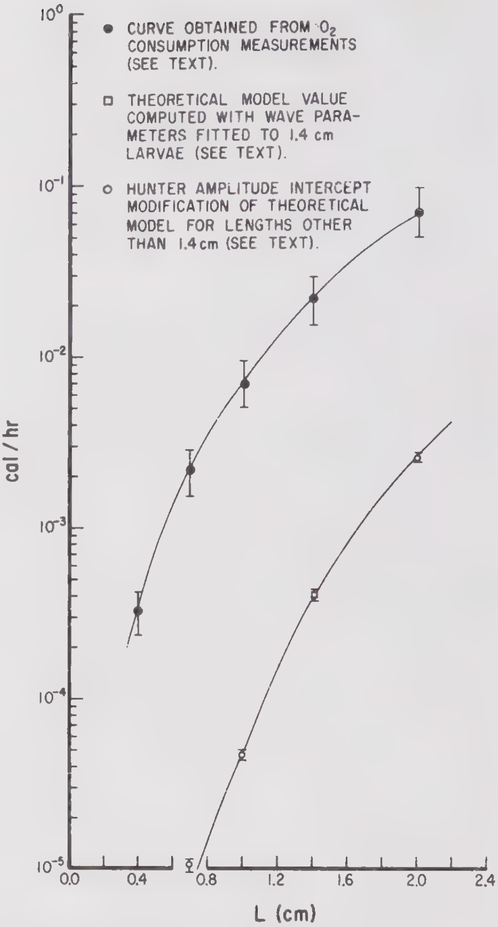

FIGURE 9.—Energy consumption of swimming based on theoretical model (open circles and open square) and total energy consumption based on O_2 utilization (closed circles) as a function of length. Vertical lines on both curves span one standard error of the data.

The evaluation of propulsive energetics as outlined in this study is directed at only one size of the anchovy larva because the method requires detailed knowledge of the various wave-form parameters as functions of time for each length of the organism studied. Valid results cannot be obtained for other sizes by a mere alteration of the length of the organism in the wave-parameter functions. By the method outlined here, the only way to properly evaluate propulsive energetic costs for different lengths would be to repeat the course of wave-parameter determination completely. However, with such limitations in mind it is interesting to compare results obtained when modification of the existing wave-parameter functions is made using extensions of known length-dependent wave-parameter quantities which have been measured for larval anchovies. The only such wave parameter available for modification and incorporation into the energy formulation is the wave amplitude.

Hunter (1972) measured the relationship between tail-beat amplitude and larval length for intermittent swimming and found the relationship,

$$A = 0.112 + 0.170L$$

where L and A are in centimeters. Since minimal amplitude dependence on length exists because of the exaggerated whiplike motion of the tail, Hunter's amplitude value is greater than my value for the maximum wave amplitude of 1.4-cm larvae. This is because amplitudes used in this study are measured as the wave crest progresses caudally at each successive time unit, whereas at the tail, wave progression ceases along the body and may even become retrograde due to the whiplike motion. The important point is the intercept at zero length where both measurements must be consistent, i.e., equal. Thus, admitting equality of the interception point at $L = 0$ and adjusting the first order coefficient in Hunter's equation to yield the correct value for maximum amplitudes at $L = 1.4$ cm we get,

$$A_{\max} = 0.112 + 0.094\ L$$

This value was substituted for $A_{\max} = 0.026\ L$ in the amplitude function $A(t) = 0.206\ L \exp [-0.044\ (t - 7.19)^2]$ and its first two derivatives used in the $L = 1.4$ cm formulation. The work integrals were then recomputed at the three new points $L = 0.4$ cm, $L = 0.7$ cm, and $L = 2.0$ cm. Because the $A_{\max}$ values coincided at $L = 1.4$ for both treatments this value was not used again in the integration procedure. The values obtained are shown in Table 2. Least squares regression of the data assuming the functional form $E = aL^b$ where E is energy/excursion in ergs and L length in centimeters yielded $E = 27.5\ L^{4.48}$. The energy/excursion calculated for the four additional lengths was then converted to hourly energy rates using the excursion frequencies cited earlier. The results obtained were plotted with scales of calories per hour vs. length in centimeters. For comparison, another curve of the form $\frac{dO_2}{dt} = f(L)$ was computed and plotted along with the curve formed using the additional model points above (Figure 9). The line shown connecting these points is fitted by eye. The comparison curve was based on the respiration value of 0.0218 cal/mg dry wt/h and the following relationship between dry weight in milligrams and length in millimeters, $\log W = 3.3237 \log L - 3.8205$ (Lasker et al., 1971). This comparison curve is isomorphic to the length-weight curve with no allowance being made for specific respiration changes with increasing weight. Therefore the curve is to be regarded as the best approximation to the total O_2 consumption rate for swimming larval anchovies. It provides only a means of judging the physiological reliability of the energy summation method employed here. However, because the changes in specific respiration as a function of weight would not change this comparison curve appreciably, it can probably be regarded as sufficiently reliable. With this understanding some comparison of these curves can be made.

TABLE 2.—Excursion energies for five larval anchovy lengths using Hunter's modified intercept amplitude function (see text for complete discussion) for extension to larval lengths other than 1.4 cm.

Length (cm)	Energy/ excursion (ergs)
2.0	881.4
1.4	144.8
1.0	16.3
0.70	3.6
0.40	0.76

From laboratory observation of larvae it seems apparent that nondimensional amplitude and wavelength do not remain constant but decrease in absolute value as length is increased. That is, functions descriptive of these nondimensional parameters do not remain descriptive of animals of all lengths. That is exactly what is observed as we deviate from the original $L = 1.4$ cm point where the nondimensional wave parameters are fitted. Even with modification of $A_{\max}$ used to compute the original curve this effect is still observable. Part of the deviation is, however, due to the behavior of the larvae as age increases. Very small larvae float 90% of the time with occasional bursts of intensive activity (Hunter, 1972) which, as I pointed out earlier, is quite inefficient. As the larvae get older, however, intermittent, more efficient swimming becomes the dominant mode of locomotion. This trend is partially reflected in these two curves. As the larvae get older and larger the intermittent swimming rate decreases and the nondimensional amplitude and wave functions decrease also. This accounts for the large locomotion energy computed for larvae greater than 1.4-cm in length. It is interesting to note how behavioral factors, when unavoidably neglected in extending this curve, become evident when compared with reasonable estimates for total energy consumption.

In view of the behavioral-mathematical factors influencing the shape of the theoretical curve in the directions observed here and the physiologic reasonableness of the metabolic swimming efficiencies obtained when exact wave parameters descriptive of the L = 1.4-cm larva are used, it is reasonable to conclude that the energies calculated from the model are the best estimates of the swimming energetic requirement per excursion of the larval anchovy, excursion being regarded as a discrete, reproducible behavioral entity, currently available.

Therefore, the major results of this study are 1) the demonstration that modifications of existing methods of computing energy of translation yield information on behavior when consideration is given to differences in behavior, shape, and flow scale, 2) that a good correlation exists in terms of metabolic swimming efficiency obtained between direct O_2 measurements and the model, 3) a confirmation of the high efficiency of large amplitude, intermittent swimming behavior, and 4) quantitative estimates of swimming energy requirements derived from this model may be used for other larval anchovy research.

Theoretical studies such as random walk analyses and correlations with feeding behavior and migration which are being studied currently could incorporate these data to provide a comprehensive and quantitative picture of larval anchovy energetics and behavior.

ACKNOWLEDGMENTS

I thank Reuben Lasker of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for proposing this study, donation of facilities, critical reading of the manuscript, and kind and constant encouragement throughout its execution. I would also like to thank John Hunter, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for numerous helpful discussions on aspects of larval behavior and loan of larval anchovy feeding films. Appreciation is also expressed to the staff of the National Marine Fisheries Service computer facility for their assistance in this project. This work was supported by NOAA, Office of Sea Grant, Department of Commerce, under grant #UCSD 04-3-158-22.

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APPENDIX

The integration of the iterated integrals was accomplished via a two-dimensional extension of the standard Gauss-Legendre guadrature. The one-dimensional fixed limit integration formula was used by Holwell and Miles (1971) for similar classes of functions with good results. The type of integrals requiring evaluation were of the general form

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt$$

a, b, fixed.

Defining

$$G(t) = \int_{f(t)}^{g(t)} F(x, t)\, dx,$$

we get

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt = \int_a^b G(t)dt.$$

By n-point Gauss-Legendre quadrature Abramovitz and Stegun (1966) this is given approximately by,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i\, G(\xi_i)$$

where $\xi_i = \dfrac{b-a}{2}\, y_i + \dfrac{b+a}{2}$

y_i = ith zero of $P_n(x)$, the n-order Legendre polynomial and

$$w_i = 2\Big/\left(1 - y_i{}^2\right) \left[P'_n(\xi_i)\right]^2 .$$

Using Gauss-Legendre quadrature on $G(\xi_i)$ yields,

$$\int_a^b G(t)dt \cong \frac{b-a}{2} \sum_{i=1}^{n} w_i \int_{f(\xi_i)}^{g(\xi_i)} F(x, \xi_i)\, dx$$

$$\cong \frac{b-a}{2} \sum_{i=1}^{n} w_i\, \frac{g(\xi_i) - f(\xi_i)}{2} \sum_{j=1}^{n} w_j^* F(\eta_j, \xi_i),$$

where $\eta_j = \dfrac{g(\xi_i) - f(\xi_i)}{2}\, y_j + \dfrac{g(\xi_i) + f(\xi_i)}{2}$

$w_j^* = 2/(1 - y_j) \left[P'_n(\eta_j)\right]^2$ and

y_j = jth root of $P_n(x)$.

We have finally the result,

$$\int_a^b \int_{f(t)}^{g(t)} F(x, t)\, dxdt \cong \frac{b-a}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} w_i\, w_{j^*} \frac{g(\xi_i) - f(\xi_i)}{2}\, F(\eta_j, \xi_i),$$

where the above definitions hold.

Some Morphometrics of Billfishes From the Eastern Pacific Ocean

PAUL G. WARES[1] and GARY T. SAKAGAWA[2]

ABSTRACT

Length-weight and morphometric data collected over 4 yr (1967-70) from sport fisheries at three eastern Pacific locations are presented for striped marlin *(Tetrapturus audax)*, sailfish *(Istiophorus platypterus)*, and blue marlin *(Makaira nigricans)*. The data were gathered from San Diego, California (U.S.A.), Buena Vista, Baja California Sur (Mexico), and Mazatlán, Sinaloa (Mexico).

Regression of eye-fork length and covariance analysis were used to compare maximum body depth, depth at vent, pectoral fin length, dorsal fin height, maxillary length, snout to mandible and snout to posterior orbit lengths between sexes and areas for each species. Regression equations are given for converting fork length and mandible-fork length to eye-fork length. Based on these conversions our Pacific Ocean data on sailfish are compared with data from the Atlantic Ocean.

Length-weight regressions using both eye-fork length and fork length are given for each species by sex.

The eastern Pacific off Mexico and southern California is probably one of the world's most productive regions for billfishes. Specimens from this region, however, have too often been underrepresented in comparative studies on billfish morphology. It is the purpose of this paper to (1) present some basic data on morphometric and meristic characters of striped marlin *(Tetrapturus audax)*, blue marlin *(Makaira nigricans)*, and sailfish *(Istiophorus platypterus)* from the eastern North Pacific Ocean, and (2) discuss some sources of variation in morphometric characters.

SAMPLING

Source of Data

The data were gathered by the staff of the Tiburon Fisheries Laboratory during 1967 through 1970. The sole source of data was the sampling of sport landings at three locations. These locations were: (1) the San Diego Marlin Club at San Diego, California; (2) Rancho Buena Vista in the territory of Baja California Sur, Mexico; and (3) the Star Fleet at Mazatlán, Sinaloa, Mexico. Sampling at these locations each year was conducted primarily during the months when billfish catches were highest. The monthly distribution of samples is shown in Table 1.

The specimens examined were almost totally fish caught on one-day trips in small boats ranging from about 6 to 12 m in length. For this reason most of the samples at each location represent fishes caught in a radius of less than about 100 km from the landing site. All of the fish were kept fresh, unfrozen, and at San Diego and Buena Vista, usually moist. The billfish landed at Mazatlán tended to be in a more dried-out condition. This made full erection of the dorsal fin difficult. Many fish were, therefore, measured when the dorsal fin was only half erect, but we feel that this did not affect the results significantly. The effect of dryness on body measurements is unknown, but we feel that it was not significant. Body length measurements were made with a steel tape. Nearly all of the fish at San Diego and a few of the fish at Mazatlán were measured while hanging by the tail. Otherwise, measurements were made while fish were lying on their side on a flat surface with heads and tails raised to horizontal. We tested the effect of hanging on eye-fork lengths of 10 fish at San Diego by measuring each one while hanging

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FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972
Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.

Table 1.--Number of blue marlin, sailfish, and striped marlin sampled in 1967-70 at Buena Vista, Mazatlán, and San Diego.

	Months											
	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Blue marlin												
Buena Vista												
Female												
1967	—	—	—	—	1	—	—	—	—	—	—	1
1969	—	—	—	—	2	7	—	—	—	5	—	14
1970	—	—	—	—	—	—	—	—	15	5	—	20
Total	—	—	—	—	3	7	—	—	15	10	—	35
Mazatlán												
Female												
1969	—	—	4	6	10	2	—	—	—	—	—	22
Sailfish												
Buena Vista												
Male												
1967	—	—	—	2	—	—	—	—	—	—	—	2
1968	—	—	—	—	3	—	—	—	—	—	—	3
1969	—	—	—	—	1	3	—	—	—	5	—	9
1970	—	—	—	—	—	—	—	—	8	6	—	14
Total	—	—	—	2	4	3	—	—	8	11	—	28
Female												
1967	—	—	—	2	4	—	—	—	—	—	—	6
1968	—	—	1	3	7	7	—	—	—	—	—	18
1969	—	—	—	10	1	9	—	—	—	—	6	26
1970	—	—	—	—	—	—	—	—	—	7	14	21
Total	—	—	1	15	12	16	—	—	—	7	20	71
Mazatlán												
Male												
1967	—	—	4	5	—	—	—	—	—	—	—	9
1968	—	—	7	44	15	—	—	—	—	—	2	68
1969	1	1	25	73	142	22	—	—	—	—	—	264
Total	1	1	36	122	157	22	—	—	—	—	2	341
Female												
1967	—	—	17	11	—	—	—	—	—	—	—	28
1968	—	—	14	64	26	—	—	—	—	—	3	107
1969	4	7	17	101	93	14	—	—	—	—	—	236
Total	4	7	48	176	119	14	—	—	—	—	3	371
Striped marlin												
Buena Vista												
Male												
1967	—	—	—	53	30	—	—	—	—	—	—	83
1968	—	—	49	64	74	34	—	—	—	—	—	221
1969	—	17	86	113	39	18	—	—	—	—	—	273
1970	—	—	—	—	—	—	—	—	6	33	1	40
Total	—	17	135	230	143	52	—	—	6	33	1	617
Female												
1967	—	—	—	46	19	—	—	—	—	—	—	65
1968	—	—	37	48	60	25	—	—	—	—	—	170
1969	—	22	51	54	42	29	—	—	—	9	—	207
1970	—	—	—	—	—	—	—	—	6	32	6	44
Total	—	22	88	148	121	54	—	—	6	41	6	486

Table 1.—Number of blue marlin, sailfish, and striped marlin sampled in 1967-70 at Buena Vista, Mazatlán, and San Diego.—Continued

	Months											
	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Mazatlan												
Male												
1967	—	—	21	7	—	—	—	—	—	—	—	28
1968	—	—	50	26	1	—	—	—	—	—	1	78
1969	13	42	30	30	5	1	—	—	—	—	—	121
1970	—	—	—	—	—	—	—	—	—	—	2	2
Total	13	42	101	63	6	1	—	—	—	—	3	229
Female												
1967	—	—	15	11	—	—	—	—	—	—	—	26
1968	—	—	31	18	—	—	—	—	—	—	4	53
1969	16	48	36	29	9	3	—	—	—	—	—	141
1970	—	—	—	—	—	—	—	—	—	—	6	6
Total	16	48	82	58	9	3	—	—	—	—	10	226
San Diego												
Male												
1967	—	—	—	—	—	—	22	50	—	—	—	72
1968	—	—	—	—	—	—	1	35	33	—	—	69
1970	—	—	—	—	—	—	—	6	—	—	—	6
Total	—	—	—	—	—	—	23	91	33	—	—	147
Female												
1967	—	—	—	—	—	—	35	126	—	—	—	161
1968	—	—	—	—	—	—	6	85	32	—	—	123
1970	—	—	—	—	—	—	3	26	2	—	—	31
Total	—	—	—	—	—	—	44	237	34	—	—	315

and then again after lying flat. The fish while hanging ranged from 1 mm shorter to 7 mm longer, the average being 3 mm longer than when lying flat. The mean difference was not significant.

Definitions of Counts and Measurements

The counts and measurements used in this study are defined below. Though the terminology is not identical, many of these are the same as those recommended by Rivas (1956).

Dorsal rays—number of rays in second dorsal fin.

Anal rays—number of rays in second anal fin.

Fork length—tip of snout to posterior margin of middle caudal rays.

Mandible-fork length—tip of mandible with mouth closed to posterior margin of middle caudal rays.

Eye-fork length—posterior margin of orbit to posterior margin of middle caudal rays.

Snout to mandible—tip of snout to tip of mandible with mouth closed.

Table 2.—Frequency of dorsal and anal fin ray counts for blue marlin, sailfish and striped marlin from the eastern Pacific.

	Number of rays						
	5	6	7	8	Total	$\bar{X}$	s
Dorsal fin rays							
Blue marlin	—	13	20	—	33	6.61	0.496
Sailfish	—	24	56	—	80	6.70	0.461
Striped marlin	10	223	14	—	247	6.02	0.312
Anal fin rays							
Blue marlin	—	5	27	1	33	6.88	0.415
Sailfish	1	29	48	1	79	6.62	0.538
Striped marlin	40	195	7	—	242	5.86	0.420

Snout to eye—tip of snout to anterior margin of orbit.

Length of maxillary—tip of mandible to posterior end of maxillary bone.

Maximum body depth—base of dorsal groove to edge of pelvic groove, in the transverse plane where this measurement is maximum (usually near base of pectorals).

Depth at vent—depth of body as described above except in the transverse plane through vent.

Length of pectoral fin—from base of first pectoral fin ray to tip of longest ray with fin folded against body.

Length of pelvic fin—from base of fin rays to tip when fin is held at slight angle from body.

Dorsal fin height—from base of first dorsal fin spine to tip of anterior lobe of first dorsal fin with fin held as nearly erect as possible (see previous section).

METHODS OF ANALYSIS

Meristic Characters

Counts of second dorsal and second anal fin rays were the only meristic characters used. It was quite evident early in the study that the number of fin rays did not vary significantly with fish size, at least for sizes of fish we examined, and that the number for a species varied within a narrow range of two to four rays (Table 2). The meristic characters were therefore eliminated from any further analyses.

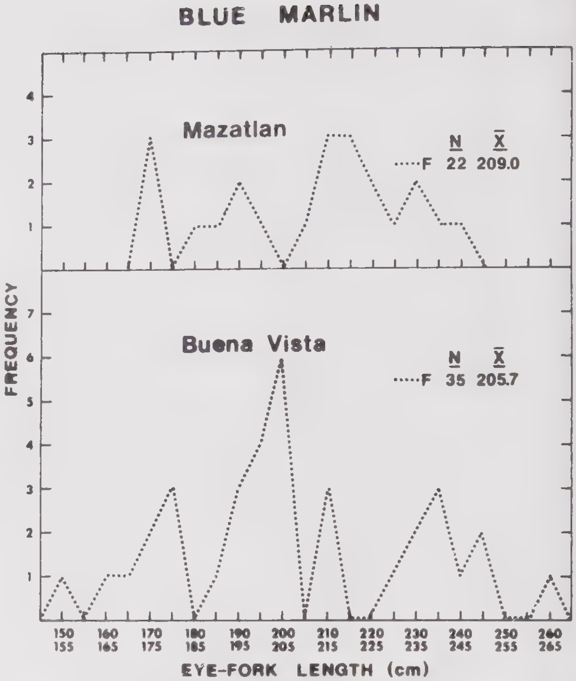

Figure 1.—Length frequency of blue marlin sampled in this study.

Morphometric Characters

Linear regression and analysis of covariance were the procedures used to analyze the data. Except for

Table 3.—Equations for converting fork and mandible-fork lengths to eye-fork length. Equations are based on $Y = a + bX$.

Relation	a	b	N	r	Range of X (cm)
Blue marlin					
Eye-fork length on fork length	−15.785	0.810	21	0.997	221.1-347.3
Eye-fork length on mandible-fork length	−5.105	0.893	22	0.979	194.0-297.6
Sailfish					
Eye-fork length on fork length	6.802	0.714	35	0.926	183.0-260.0
Eye-fork length on mandible-fork length	2.637	0.852	35	0.940	155.5-225.0
Fork length on eye-fork length	24.677	1.200	35	0.926	
Striped marlin					
Eye-fork length on fork length	−1.319	0.745	127	0.745	178.5-268.8
Eye-fork length on mandible-fork length	1.306	0.840	125	0.985	151.6-238.2

Table 4.—Coefficients of the weight-length relation for blue marlin, sailfish, and striped marlin from the eastern Pacific. (log weight = *a* + *b* (log length)).

Species	Measurement						
	Length (cm)	Weight	*a*	*b*	Range of length (cm)	*N*	*r*
Blue marlin							
Female	Eye-fork	kg	−5.690	3.318	154.0-265.1	57	0.948
	Eye-fork	lb	−5.347	3.318	154.0-265.1	57	0.948
	Snout-fork	kg	−7.543	3.905	221.1-347.3	20	0.954
	Snout-fork	lb	−7.199	3.905	221.1-347.3	20	0.954
Sailfish							
Male	Eye-fork	kg	−4.396	2.643	115.1-196.5	367	0.867
	Eye-fork	lb	−4.057	2.643	115.1-196.5	367	0.867
	Snout-fork	kg	−5.286	2.873	183.0-260.2	24	0.910
	Snout-fork	lb	−4.946	2.873	183.0-260.2	24	0.910
Female	Eye-fork	kg	−4.084	2.507	123.1-221.7	435	0.812
	Eye-fork	lb	−3.739	2.507	123.1-221.7	435	0.812
	Snout-fork	kg	−4.059	2.356	201.7-271.0	47	0.835
	Snout-fork	lb	−3.714	2.356	201.7-271.0	47	0.835
Combined sexes	Eye-fork	kg	−4.360	2.628	115.1-221.7	802	0.846
	Eye-fork	lb	−4.017	2.628	115.1-221.7	802	0.846
	Snout-fork	kg	−4.788	2.662	183.0-271.0	71	0.890
	Snout-fork	lb	−4.446	2.662	183.0-271.0	71	0.890
Striped marlin							
Male	Eye-fork	kg	−5.005	2.999	119.6-202.6	975	0.877
	Eye-fork	lb	−4.664	2.999	119.6-202.6	975	0.877
	Snout-fork	kg	−5.166	2.903	172.0-261.0	220	0.780
	Snout-fork	lb	−4.857	2.903	172.0-261.0	220	0.780
Female	Eye-fork	kg	−5.243	3.113	110.0-215.1	1,007	0.854
	Eye-fork	lb	−4.900	3.113	110.0-215.1	1,007	0.854
	Snout-fork	kg	−5.267	2.950	153.0-271.0	315	0.778
	Snout-fork	lb	−4.914	2.950	153.0-271.0	315	0.778
Combined sexes	Eye-fork	kg	−5.157	3.071	110.0-215.1	1,982	0.864
	Eye-fork	lb	−4.816	3.071	110.0-215.1	1,982	0.864
	Snout-fork	kg	−5.340	2.982	153.0-271.0	535	0.784
	Snout-fork	lb	−5.007	2.982	153.0-271.0	535	0.784

weight-length relations, transformations of the data were not necessary because plots of the data on eye-fork length indicated that they were reasonably linear. Equations for converting fork length and mandible-fork length are given in Table 3.

The equation used in the analyses, except that for weight, was $Y = a + bX$, where Y = morphometric character measured in centimeters, and a and b = constants that are determined by least-squares procedures. For weights, the equation $\log Y = a + b \log X$, where Y = weight, X = body length, and a and b = constants, was used. Weight-length relations based on weight in kilograms and pounds and body length as eye-fork length and snout-fork length are summarized in Table 4 for blue marlin, sailfish, and striped marlin. Statistical tests were performed to test the hypotheses that the intercept of the regression, a, is zero and that the slope of the regression, b, is zero for all regressions except those for weight-length.

All plots of the data were based on averages of 5-cm groupings of eye-fork length.

BLUE MARLIN

A total of 57 blue marlin was sampled at Buena Vista and Mazatlán. The average length was 206 cm at Buena Vista and 209 cm at Mazatlán (Fig. 1).

Table 5.—Regression of morphometric character on eye-fork length (cm) for blue marlin from the eastern Pacific. Weight-length relation is based on log transformed data ($\log Y = a + b\log X$); all other relations are based on untransformed data ($Y = a + bX$). Data are for females. (* = 5% significance level; ** = 1% significance level).

Character	*a*	*b*	Range *x*	Range *Y*	*N*
Buena Vista					
Weight (kg)	−5.960	3.433	154.0-265.1	40.9-244.9	35
Maximum body depth (cm)	−5.887	0.245**	154.0-239.8	32.2- 53.6	14
Length of pectoral fin (cm)	18.594**	0.163**	154.0-265.1	40.7- 62.0	35
Length of pelvic fin (cm)	37.244**	0.003	154.0-239.8	32.1- 45.3	14
Dorsal fin height (cm)	20.966**	0.084**	154.0-265.1	31.0- 49.4	34
Length of maxillary (cm)	15.236**	0.090**	154.0-265.1	25.9- 40.2	34
Number of dorsal fin rays	6.468**	0.001	154.0-265.1	6-7	33
Number of anal fin rays	5.286	0.008**	154.0-265.1	6-8	33
Mazatlán					
Weight (kg)	−4.972	3.011	171.4-242.2	46.7-171.5	22
Length of pelvic fin (cm)	57.859**	0.096*	171.4-242.2	30.1- 45.3	22
Dorsal fin height (cm)	7.560	0.150**	171.4-242.2	32.2- 45.9	22
Length of maxillary (cm)	4.014	0.140**	171.4-242.2	26.5- 40.2	21

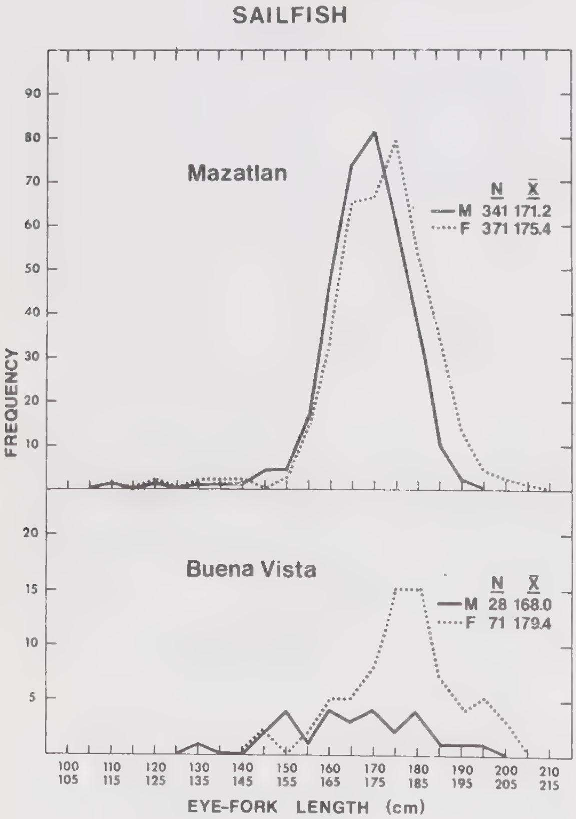

Figure 2.—Length frequency of sailfish sampled in this study.

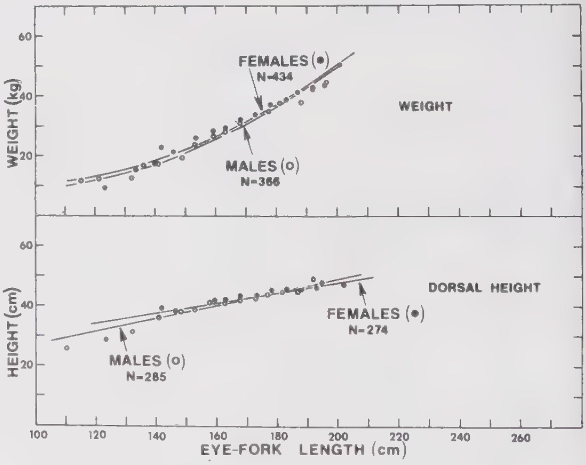

Figure 3.—Weight and dorsal height as a function of eye-fork length of sailfish from the eastern North Pacific.

Samples from both locations consisted of only females. We have no adequate explanation for this phenomenon; however, we note that in the central Pacific, which is west of our sampling area, more males than females are generally caught in the sport fishery (Strasburg, 1969). In the longline fishery sex ratios vary greatly both temporally and spatially (Kume and Joseph, 1969).

Regressions of each of the characters as a function of eye-fork length are shown in Table 5. Ex-

Table 6.—Results of analysis of covariance of morphometric character as a function of eye-fork length. The statistical test is whether the relation is significantly different among areas. (n.s. = not significant; * = 5% significance level; ** = 1% significance level).

Character	Blue marlin	Sailfish		Striped marlin	
	Female	Male	Female	Male	Female
Weight	n.s.	n.s.	n.s.	**	**
Maximum body depth	—	n.s.	*	**	**
Depth at vent	—	n.s.	n.s.	**	**
Length of pectoral fin	—	n.s.	n.s.	**	**
Length of pelvic fin	n.s.	n.s.	n.s.	n.s.	**
Snout to mandible length	—	n.s.	n.s.	**	**
Snout to eye length	—	—	*	*	**
Dorsal fin height	n.s.	n.s.	*	*	**
Length of maxillary	n.s.	n.s.	n.s.	n.s.	n.s.

cluding results for weight-length relations, results of the statistical test of $a = 0$ indicate that most of the a's are significantly different from zero. This suggests that growth of the body parts is allometric, or the parts do not grow as a constant proportion to body size, which is characteristic for most body parts of fishes (Martin. 1949).

Analysis of covariance was performed to test whether the regressions differed between sampling locations. No significant differences were found (Table 6). Samples from Buena Vista and Mazatlán were therefore pooled and the regressions were recalculated (Table 7).

SAILFISH

A total of 811 sailfish was sampled at Buena Vista and Mazatlán. Sampling at Buena Vista was in 1967-70 and at Mazatlán, only in 1967-69. More fish, however, were sampled at Mazatlán than at

Table 7.—Regression of morphometric character on eye-fork length (cm) for pooled (locations and sexes) samples of blue marlin and sailfish from the eastern Pacific. Weight-length relation is based on log transformed data ($\log Y = a + b \log X$); all other relations are based on untransformed data ($Y = a + bX$).

Character	a	b	Range of length	N
Blue marlin				
Weight (kg)	−5.690	3.318	154.0-265.1	57
Maximum body depth (cm)	−5.887	0.245	154.0-239.8	14
Length of pectoral fin (cm)	18.594	0.163	154.0-265.1	35
Length of pelvic fin (cm)	49.263	−0.056	154.0-242.2	36
Dorsal fin height (cm)	17.129	0.103	154.0-265.1	56
Length of maxillary (cm)	12.366	0.103	154.0-265.1	55
Sailfish				
Weight (kg)	−4.360	2.628	115.1-221.7	802
Maximum body depth (cm)	2.824	0.150	121.5-221.7	239
Depth at vent (cm)	10.160	0.073	121.5-221.7	239
Length of pectoral fin (cm)	0.703	0.211	121.5-221.7	279
Length of pelvic fin (cm)	12.171	0.274	115.1-203.0	529
Snout to mandible length (cm)	16.382	0.099	133.2-203.0	196
Snout to eye length (cm)	24.707	0.207	156.0-203.0	34
Dorsal fin height (cm)	8.292	0.202	115.1-203.0	559
Length of maxillary (cm)	9.910	0.110	115.1-203.0	553

Table 8.—Regression of morphometric character on eye-fork length (cm) for sailfish from the eastern Pacific. Weight-length relation is based on log transformed data ($\log Y = a + b \log X$); all other relations are based on untransformed data ($Y = a + bX$). (* = 5% significance level; ** = 1% significance level).

Character	Male					Female				
			Range					Range		
	a	*b*	*X*	*Y*	*N*	*a*	*b*	*X*	*Y*	*N*
Buena Vista										
Weight (kg)	−4.825	2.829	133.4-196.5	13.4-47.5	28	−4.291	2.601	146.3-203.0	20.4-54.1	70
Maximum depth (cm)	2.163	0.156**	160.9-182.9	27.8-31.3	5	14.000**	0.092**	161.5-203.0	28.6-35.0	24
Depth at vent (cm)	−11.300	0.194	160.9-182.9	19.8-26.9	5	15.743**	0.043	161.5-203.0	20.3-26.4	24
Length of pectoral fin (cm)	7.181	0.174**	133.4-196.5	27.0-44.5	21	6.997	0.181**	146.3-203.0	29.8-47.4	49
Length of pelvic fin (cm)	17.612	0.248**	152.1-182.5	54.9-64.7	8	17.844	0.239**	147.2-203.0	52.0-70.0	24
Snout to mandible length (cm)	9.092	0.131**	160.9-182.9	30.5-33.3	5	4.060	0.167*	166.0-203.0	28.0-41.3	19
Snout to eye length (cm)	—	—	—	—	—	−72.145	0.692**	187.5-203.0	56.5-68.0	4
Dorsal fin height (cm)	10.713	0.178**	133.4-196.5	30.5-50.6	22	16.723**	0.151**	146.3-203.0	37.3-51.4	46
Length of maxillary (cm)	10.609**	0.103**	133.4-196.5	23.4-32.0	21	8.903**	0.116**	146.3-203.0	23.8-32.1	46
Number of dorsal fin rays	6.316**	0.002	133.4-196.5	6-7	22	−5.446**	0.008	146.3-193.4	6-7	35
Number of anal fin rays	5.190**	0.009	133.4-196.5	6-8	21	6.350**	0.001	146.3-193.4	6-7	35
Mazatlán										
Weight (kg)	−4.291	2.594	115.1-193.5	11.7-47.2	339	−4.020	2.479	123.1-221.7	9.9-50.6	365
Maximum depth (cm)	−0.443	0.168**	121.5-190.0	19.4-34.5	77	4.196	0.141**	133.2-221.4	20.4-39.1	133
Depth at vent (cm)	8.144**	0.086**	121.5-190.0	18.2-33.9	77	10.246**	0.073**	133.2-221.7	17.9-26.8	133
Length of pectoral fin (cm)	−8.092	0.259**	121.5-190.0	20.4-43.3	77	3.954	0.192**	133.2-221.7	26.8-45.9	132
Length of pelvic fin (cm)	11.830**	0.275**	115.1-193.5	37.9-67.7	263	12.156**	0.275**	123.1-195.8	44.9-71.6	234
Snout to mandible length (cm)	14.063	0.110*	135.6-190.0	21.4-41.2	63	22.401**	0.066*	133.2-194.1	25.4-41.1	109
Snout to eye length (cm)	27.064	0.180	167.3-184.4	49.5-64.3	8	17.135	0.260**	156.0-187.1	56.0-71.0	22
Dorsal fin height (cm)	5.539	0.217**	115.1-193.5	25.5-52.4	263	11.965**	0.184**	123.1-195.8	29.1-62.8	228
Length of maxillary (cm)	8.746**	0.116**	115.1-193.5	21.1-39.1	260	12.196**	0.097**	123.1-195.8	20.8-32.3	226
Number of dorsal fin rays	7.243*	0.003	149.2-181.6	6-7	12	3.175	0.019	142.1-191.4	6-7	11
Number of anal fin rays	4.083	0.015	149.2-181.6	6-7	12	4.110	0.014	142.1-191.4	5-7	11

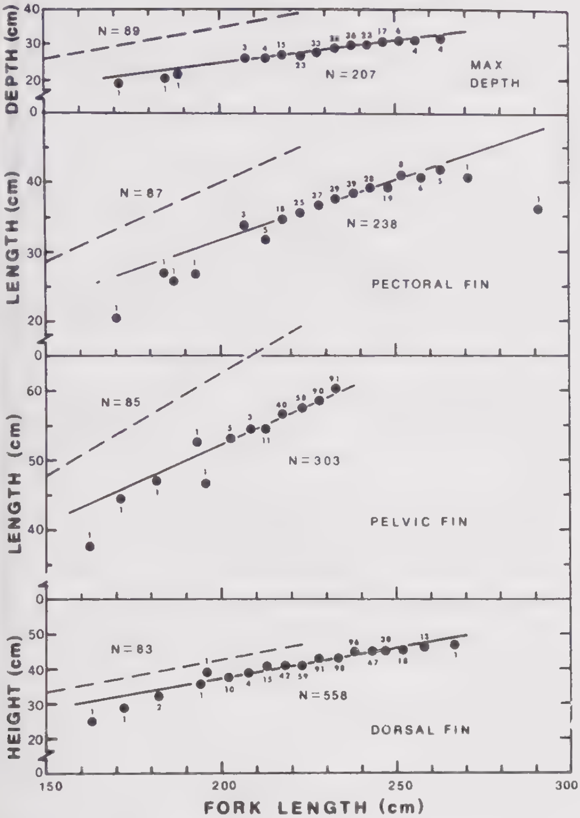

Figure 4.—Comparison of regressions of morphometric characters on fork length of sailfish from the Atlantic (dashed line) and the eastern North Pacific (solid line). Numbers indicate sample sizes for points.

Buena Vista (Table 1). At both sampling locations the sizes of sailfish were quite similar, although the females averaged 179 cm long and the males 168 cm long (Fig. 2). Between locations the size differences are statistically significant only for females.

Location and Sex Differences

Analysis of covariance was used to test whether for each sex the regressions (Table 8) were significantly different between locations (Table 6). Because there was no trend in the results, we assumed that there were no location differences and pooled the data from the two locations. We then used analysis of covariance to test whether there were differences between sexes. Only weight-length and dorsal fin height-length relations proved to be significantly different between sexes. Females were heavier for a given length than males, and females under about 160 cm long had a taller dorsal fin than males (Fig. 3). For fish larger than 160 cm long, the males had a taller dorsal fin. However, there is considerable overlap in the data for males and females, and probably the difference between sexes would disappear if a larger sample of fish were analyzed. Regressions based on the pooled data are shown in Table 7.

Comparison with Atlantic Sailfish

Morrow and Harbo (1969) analyzed meristic and morphometric measurements of sailfish from several locations in the Atlantic and Pacific Oceans. They found that the characters were similar for fish from both oceans and they therefore concluded that specimens from the two oceans belong to the same species. We used Morrow and Harbo's data from the Atlantic for comparison with our data, which provides a larger sample from the eastern Pacific

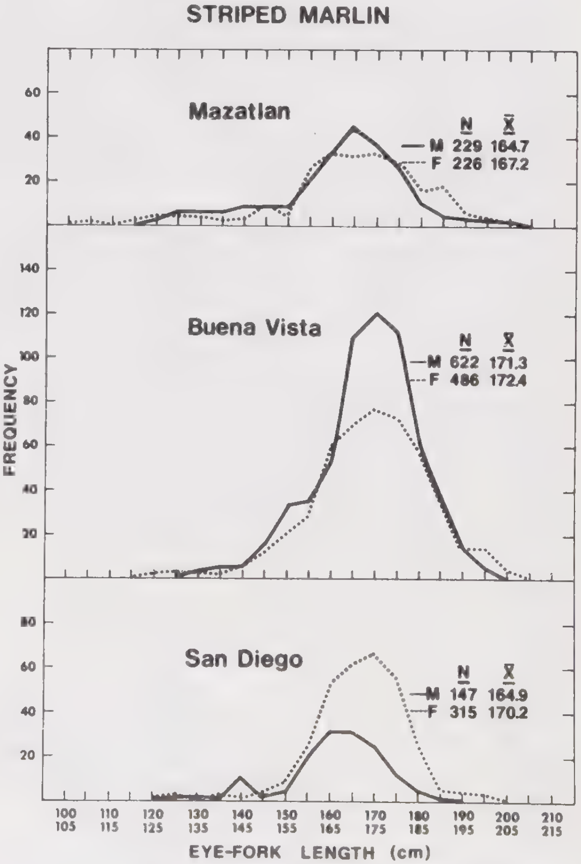

Figure 5.—Length frequency of striped marlin sampled in this study.

Table 9.—Regression of morphometric character on eye-fork length (cm) for striped marlin from the eastern Pacific. Weight-length relation is based on log transformed data (log $Y = a + b \log X$); all other relations are based on untransformed data ($Y = a + bX$). (* = 5% significance level; ** = 1% significance level).

Character	Male					Female				
			Range					Range		
	a	*b*	*X*	*Y*	*N*	*a*	*b*	*X*	*Y*	*N*
Buena Vista										
Weight (kg)	−5.294	3.126	119.6-202.0	13.1-91.4	601	−5.420	3.183	125.0-215.1	16.9-101.3	472
Maximum depth (cm)	2.463*	0.178**	123.1-202.0	22.1-39.5	321	1.206	0.187**	125.0-215.1	22.9- 40.6	246
Depth at vent (cm)	−3.250*	0.173**	123.1-202.0	16.4-39.3	301	−1.618	0.165**	125.0-215.1	17.5- 37.8	232
Length of pectoral fin (cm)	2.557	0.242**	123.1-202.0	27.3-52.5	368	−2.124	0.273**	125.0-215.1	29.4- 59.0	303
Length of pelvic fin (cm)	41.864**	−0.041*	119.6-199.5	22.7-43.5	273	34.995**	0.006	126.9-201.4	7.5- 45.1	202
Snout to mandible length (cm)	13.376**	0.099**	123.1-202.0	15.6-41.0	280	14.324**	0.095**	125.0-215.1	22.0- 39.5	207
Snout to eye length (cm)	16.502**	0.260**	131.4-189.0	47.0-69.4	81	15.136**	0.267**	125.0-197.5	45.0- 73.0	64
Dorsal fin height (cm)	10.176**	0.171**	119.6-199.5	26.9-46.0	316	7.829	0.188	128.1-201.4	31.0- 47.2	246
Length of maxillary (cm)	5.369**	0.167**	119.6-199.5	22.9-41.3	311	5.054	0.170**	126.9-201.4	24.5- 46.2	248
Number of dorsal fin rays	6.527**	−0.003	131.0-195.2	5-7	101	5.438**	0.003	126.9-201.4	5-7	108
Number of anal fin rays	5.949	−0.001	131.0-195.2	5-7	91	5.228**	0.004	126.9-201.4	5-7	105
Mazatlán										
Weight (kg)	−5.183	3.064	120.4-202.6	15.8-73.5	227	−5.119	3.034	110.0-204.5	10.3- 86.5	222
Maximum depth (cm)	−5.508**	0.218**	124.0-200.0	20.1-36.3	104	−1.341	0.193**	116.8-204.5	22.4- 41.2	76
Depth at vent (cm)	−0.902	0.154**	124.0-200.0	16.0-29.0	104	0.588	0.144**	116.8-204.5	14.6- 32.3	76
Length of pectoral fin (cm)	−8.151**	0.302**	124.0-200.0	28.7-49.8	106	2.858	0.239**	116.8-204.5	24.0- 52.1	83
Length of pelvic fin (cm)	37.680**	0.010	120.4-202.6	21.5-44.1	118	30.045**	0.041	110.0-197.0	15.6- 45.2	136
Snout to mandible length (cm)	13.427**	0.095**	124.5-191.6	22.0-36.8	73	16.211**	0.079**	116.8-197.0	20.0- 35.2	51
Snout to eye length (cm)	7.285	0.306**	124.0-191.6	37.7-69.4	27	29.190**	0.179**	129.0-204.5	49.0- 68.0	24
Dorsal fin height (cm)	12.680**	0.155**	126.4-202.6	27.8-47.5	50	8.693*	0.180**	118.9-197.0	28.4- 48.4	61
Length of maxillary (cm)	7.467**	0.153**	120.4-202.6	22.4-38.0	107	8.380**	0.150**	118.9-197.0	25.1- 39.5	127
Number of dorsal fin rays	—	—	—	—	—	6	0	157.3-190.1	6	7
Number of anal fin rays	−1.244	0.040	170.7-180.2	5-6	3	6	0	157.3-190.1	6	7
San Diego										
Weight (kg)	−4.060	2.608	129.4-191.0	29.5-83.9	147	−4.574	2.843	127.0-203.3	22.2-103.4	313
Maximum depth (cm)	12.928**	0.120**	129.4-191.0	28.4-41.2	141	8.457**	0.153**	135.0-201.5	27.1- 46.9	284
Depth at vent (cm)	5.599**	0.129**	129.4-191.0	21.3-32.3	141	1.449	0.157**	135.0-201.5	21.0- 35.1	283
Length of pectoral fin (cm)	14.110**	0.164**	129.4-191.0	32.2-50.1	146	7.695**	0.209**	127.0-203.3	27.9- 53.2	315
Length of pelvic fin (cm)	—	—	—	—	—	—	—	—	—	—
Snout to mandible length (cm)	17.549**	0.075**	133.7-191.0	24.8-37.4	129	15.066**	0.095**	135.0-201.5	24.3- 39.8	267
Snout to eye length (cm)	27.478**	0.196**	133.7-182.7	50.4-68.1	66	19.784**	0.248**	135.0-192.5	50.6- 75.0	152
Dorsal fin height (cm)	1.095	0.207	158.2-183.0	33.6-41.0	5	2.771*	0.202**	127.0-203.3	27.5- 44.0	29
Length of maxillary (cm)	10.295	0.133	158.2-183.0	30.7-36.6	5	10.191**	0.144**	127.0-203.3	27.6- 40.1	28
Number of dorsal fin rays	—	—	—	—	—	6.272**	−0.002	127.0-203.3	5-7	31
Number of anal fin rays	8.775	−0.017	158.2-183.0	5-6	5	6.270**	−0.001	127.0-203.3	6-7	31

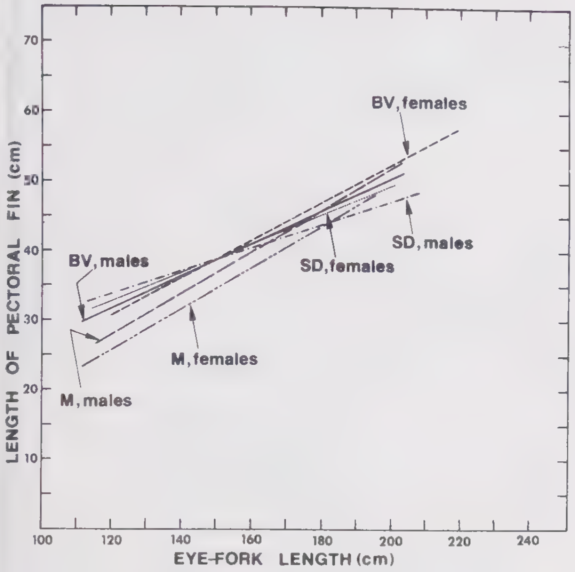

Figure 6.—Plotted regressions of pectoral fin length on eye-fork length of striped marlin by sex and locality. BV=Buena Vista, M=Mazatlán, SD=San Diego.

than was available to them (they had data on nine specimens from the coast of Peru). Body length for the Atlantic specimens was measured as fork length. In order to have the data comparable to our data, it was necessary to convert eye-fork length of our samples to fork length with the appropriate equation in Table 3.

Maximum body depth, length of pectoral fin, length of pelvic fin, and dorsal fin height were examined (Fig. 4). Analysis of covariance was not used to test for significant differences in these characters between Atlantic and eastern Pacific sailfish because of the complication of one set of data being based on converted lengths. However, we feel from visual inspection that there is sufficient separation between the regressions (especially the first three) to suggest that eastern Pacific sailfish differ significantly from Atlantic sailfish in morphometric measurements. More information based on a wide range of sizes of fish from the Atlantic and Pacific is needed for a more complete comparision.

STRIPED MARLIN

The eastern Pacific is apparently a center of high concentration of striped marlin. Considerable numbers of fish are annually caught by the commercial longline fleet and by sportsmen. In 1967-70 we sampled 2,020 specimens from the sport landings at Buena Vista, Mazatlán, and San Diego. Length frequencies of the samples are shown in Figure 5.

Location and Sex Differences

Regressions of each meristic and morphometric character as a function of eye-fork length are shown in Table 9. Analysis of covariance was performed on the data, sexes separate, to determine whether the regressions were significantly different among locations. The results (Table 6) indicated that the regressions were different. Analysis of covariance was also used to determine whether the relations were significantly different between sexes, within location. The results (Table 10) for this series of tests showed either no differences or inconsistency from one location to another, except for the relation of length of pectoral fin on eye-fork length. For this relation, significant differences between sexes were found at all three locations. The regressions are shown in Figure 6. On the basis of these results, except for pectoral fin length, it was assumed that there is no significant difference between sexes, but a significant difference among locations. The data were pooled accordingly and regressions recalculated (Table 11).

A plot of weight on eye-fork length for striped marlin from each location (Fig. 7) shows that for a given length, striped marlin from San Diego were heavier than fish from Buena Vista or Mazatlán.

Table 10.—Results of covariance analysis of morphometric character of striped marlin as a function of eye-fork length to test whether the relations are significantly different between sexes. (n.s. = not significant; * = 5% significance level; ** = 1% significance level).

Character	Buena Vista	Mazatlán	San Diego
Weight	n.s.	n.s.	n.s.
Maximum body depth	*	n.s.	**
Depth at vent	n.s.	n.s.	*
Length of pectoral fin	**	*	**
Length of pelvic fin	**	n.s.	—
Snout to mandible length	n.s.	n.s.	**
Snout to eye length	n.s.	n.s.	n.s.
Dorsal fin height	**	n.s.	n.s.
Length of maxillary	n.s.	n.s.	*

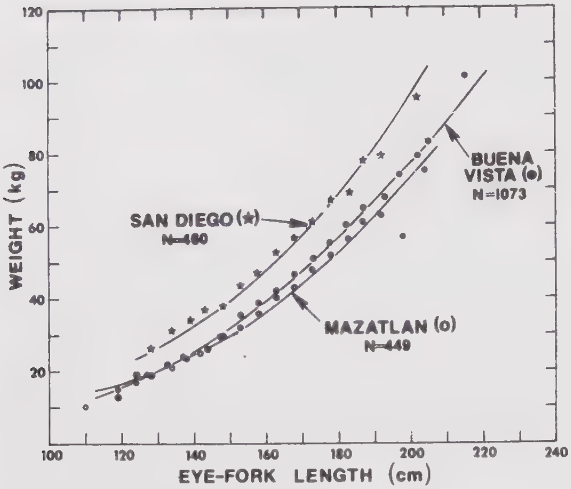

Figure 7.—Weight as a function of eye-fork length of striped marlin from the eastern North Pacific.

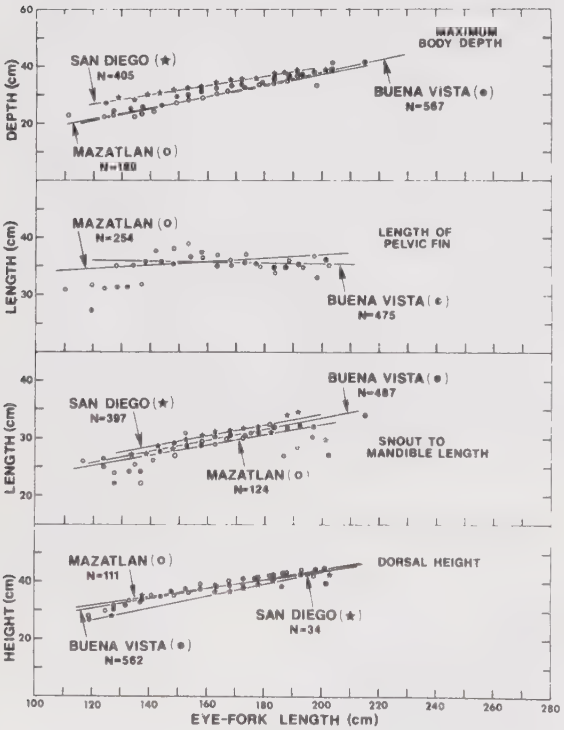

Figure 8.—Morphometric characters as a function of eye-fork length of striped marlin from the eastern North Pacific.

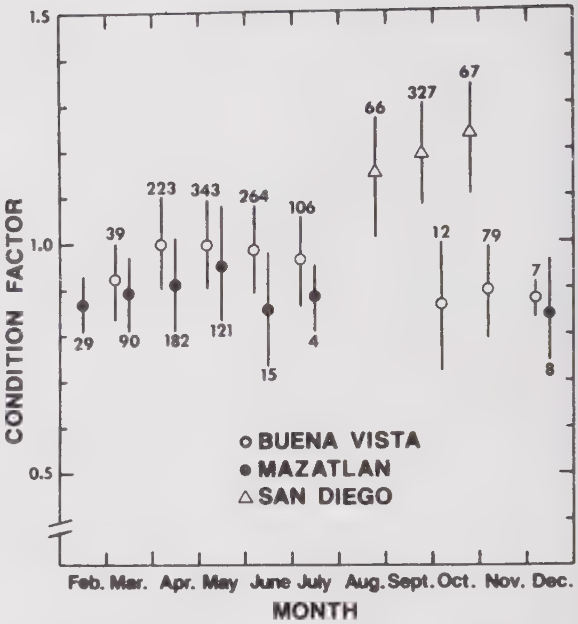

Figure 9.—Average condition factor by month for striped marlin from the eastern North Pacific. One standard deviation on each side of the mean and the sample size shown. Condition factor=W×$10^5/L^3$ where W=whole fish weight in kg and L=eye-fork length in cm.

This difference is also evident in the relation of maximum body depth on eye-fork length (Fig. 8); body depth is larger in San Diego fish. It was uncertain whether this difference was a seasonal phenomenon since San Diego samples were obtained only from August to October, months of the year when there were almost no samples from Buena Vista or Mazatlán (Table 1). Plots of condition factors by month for the three areas (Fig. 9), however, show that seasonal variation is unlikely to be the cause.

Some other relations are shown in Figure 8. They indicate that there is much overlap in the data. It thus appears that characters, other than perhaps weight, maximum body depth, and pectoral fin length, are not different enough to be useful as single diagnostic characters for separating striped marlin into location of capture.

Comparison with Other Studies

Kamimura and Honma (1958) examined five morphometric characters of striped marlin caught in the Pacific by the Japanese longline fleet. They dis-

Table 11.—Regression of morphometric character on eye-fork length (cm) for pooled (sexes) samples of striped marlin from the eastern Pacific. Weight-length relation is based on log transformed data (log $Y = a + b \log X$); all other relations are based on untransformed data ($Y = a + bX$).

Character	a	b	Range of length (cm)	N
Buena Vista				
Weight (kg)	−5.356	3.154	119.6-215.1	1073
Maximum body depth (cm)	1.578	0.184	123.1-215.1	567
Depth at vent (cm)	−2.669	0.170	123.1-215.1	533
Length of pectoral fin (cm)	−0.333	0.261	123.1-215.1	671
Length of pelvic fin (cm)	38.797	−0.020	119.6-201.4	475
Snout to mandible length (cm)	13.656	0.098	123.1-215.1	487
Snout to eye length (cm)	15.750	0.264	125.0-197.5	145
Dorsal fin height (cm)	9.171	0.178	119.6-201.4	562
Length of maxillary (cm)	5.234	0.169	119.6-201.4	559
Mazatlán				
Weight (kg)	−5.143	3.045	110.0-204.5	449
Maximum body depth (cm)	−3.642	0.207	116.8-204.5	180
Depth at vent (cm)	−0.038	0.148	118.8-204.5	180
Length of pectoral fin (cm)	−3.225	0.274	116.8-204.5	189
Length of pelvic fin (cm)	33.018	0.021	110.0-202.6	254
Snout to mandible length (cm)	14.556	0.088	116.8-197.0	124
Snout to eye length (cm)	19.061	0.236	124.0-204.5	51
Dorsal fin height (cm)	10.526	0.169	118.9-202.6	111
Length of maxillary (cm)	7.840	0.152	118.9-202.6	234
San Diego				
Weight (kg)	−4.439	2.781	127.0-203.3	460
Maximum body depth (cm)	8.400	0.152	129.4-201.5	425
Depth at vent (cm)	2.245	0.152	129.4-201.5	424
Length of pectoral fin (cm)	8.262	0.204	127.0-203.3	461
Snout to mandible length (cm)	14.363	0.097	133.7-201.5	397
Snout to eye length (cm)	21.302	0.238	133.7-192.5	218
Dorsal fin height (cm)	2.534	0.203	127.0-203.3	34
Length of maxillary (cm)	10.017	0.144	127.0-203.3	33

covered that the length of the pectoral fin was significantly longer in fish caught in the South Pacific (lat. 18°-25°S) than in the North Pacific (lat. 30°-35°N). In Figure 10, we have superimposed Kamimura and Honma's equations on a band that represents the equations calculated from our data on pectoral fin lengths. The North Pacific sample is most similar to ours, which is from about lat. 20°-35°N. The South Pacific fish, on the other hand, have definitely longer pectoral fins than our samples, but only for fish less than about 210 cm long.

Data on length of pectoral fin for nine striped marlin (for which eye-fork length was available) reported by Royce (1957) from the central and eastern equatorial Pacific are also plotted in Figure 10. The plots indicate that either there is mixing in the central Pacific of the presumed South and North Pacific stocks of striped marlin or Kamimura and Honma's samples did not adequately reflect the degree of variability in length of pectoral fin of fish from the North and South Pacific.

SUMMARY AND CONCLUDING REMARKS

Morphometric data for 57 female blue marlin are presented; comparisons with fish from other areas were omitted due to the small sample size. For sailfish it appears that characters such as maximum

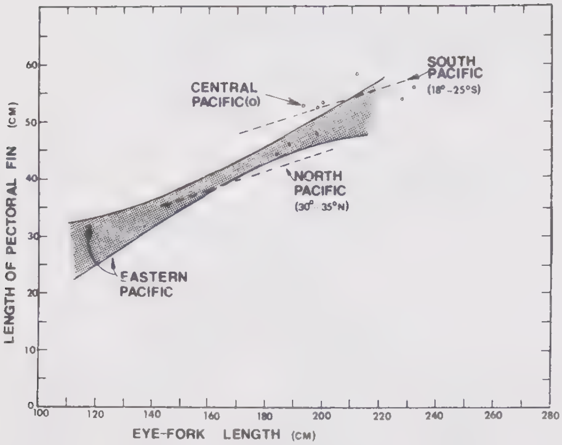

Figure 10.—Comparison of pectoral fin of striped marlin stocks in the Pacific Ocean. The shaded band represents the area in which our data for the relations of eastern Pacific fish fall. Data for South and North Pacific fish are from Kamimura and Honma (1958). Data for central Pacific fish are from Royce (1957).

body depth, length of pectoral fin, length of pelvic fin, and dorsal fin height are considerably shorter on the average in fish from the eastern Pacific than in fish of identical size from the Atlantic Ocean. For striped marlin, our results indicated that weight and maximum body depth can be used to separate striped marlin stocks within our study area. For example, a 180 cm long striped marlin landed off San Diego is, on the average, about 19% heavier and has a maximum body depth 3% greater than a striped marlin of identical size landed off Buena Vista or Mazatlán. Also, striped marlin from the northeastern Pacific (lat. 20°-35°N) and South Pacific (lat. 18°-25°S), apparently can be separated on the basis of length of pectoral fin.

We conclude, therefore, that there are morphometric characters that can be used to separate, with some degree of accuracy, sailfish and striped marlin stocks. We suggest, however, that more powerful techniques, such as multivariate analyses, be used in future attempts of stock identification of eastern Pacific billfishes.

ACKNOWLEDGMENT

We are grateful for the generous cooperation of the staff and sportsmen at Rancho Buena Vista, the Star Fleet in Mazatlán, and the San Diego Marlin Club for permitting us to measure specimens. Larry Coe, Dan Eilers. Douglas Evans, Maxwell Eldridge, and David Tolhurst helped collect the data and Brad Cowell assisted with data processing.

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Landings of Billfishes in the Hawaiian Longline Fishery

HOWARD O. YOSHIDA[1]

ABSTRACT

The landings of the Hawaiian longline fishery are dominated by the tunas. During 1964 to 1967, the tunas, by weight, made up an average of 66% of the catch, whereas the marlins and swordfish, *Xiphias gladius*, comprised about 34%. The catch of billfishes is composed of the striped marlin, *Tetrapturus audax*, blue marlin, *Makaira nigricans*, black marlin, *M. indica*, sailfish, *Istiophorus platypterus*, shortbill spearfish, *T. angustirostris*, and swordfish.

The annual landings of blue marlin ranged between 47 and 366 metric tons during 1952 to 1970. The annual landings of striped marlin fluctuated between 93 and 228 metric tons during the same period. The blue marlin dominated the catch from 1952 to 1961. Subsequent to 1963, the billfish catches have been dominated by the striped marlin.

The monthly landings and the monthly catch rates of blue marlin and striped marlin showed similar trends. The monthly landings of striped marlin, however, showed greater fluctuations than the monthly catch per unit of effort. This was attributed in part to a change in the size composition of striped marlin in the third quarter.

The Hawaiian longline fishery has been described in the past primarily from the viewpoint of a fishery for deep-swimming tunas, usually yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*. June (1950), Otsu (1954), Shomura (1959), and Hida (1966) all have made studies on this fishery as it related to the tunas. One of the exceptions is a paper by Strasburg (1970) on the billfishes of the central Pacific Ocean, in which he briefly discussed the billfishes landed in Hawaii. This report considers the Hawaiian longline fishery as it relates to the billfishes, particularly the blue marlin, *Makaira nigricans*, and the striped marlin, *Tetrapturus audax*, primarily during the period from 1963 to 1970.

The data used for this report came primarily from two sources. The billfish landing data through 1968 were obtained from the Fishery Statistics of the United States. The landing data for 1969 and 1970 and fishing trip data are from the files of NMFS (National Marine Fisheries Service), Honolulu, Hawaii. Billfish weight and sex data from 1964 to the middle of 1970 were collected at the Honolulu auction markets by samplers from our Laboratory.

DESCRIPTION OF THE FISHERY

The Hawaiian longline fishery is the only American fishery employing the longline method of fishing (Shomura, 1959). The history and description of the fishery are given by June (1950) and Otsu (1954).

Typical Hawaiian longline boats evolved from the Japanese sampan-type, live-bait boat (June, 1950). They are characterized by a narrow bow, angular lines and a low freeboard aft. The overall length of these vessels ranges from 8.53 to 18.90 m (28 to 62 ft). All except one of the vessels in the Hawaiian fishery have wooden hulls. The length of a fishing trip averages 8 or 9 days for a Honolulu-based vessel and the majority of the trips are made within sight of the main Hawaiian Islands (Shomura, 1959).

The number of longline boats in the Hawaiian fleet has steadily declined over the years. In 1952 there were 42 boats in the Hawaiian fishery. In 1964 the number was down to 31 and in 1970 to 20. Although the number of boats in the fishery has been declining, one new boat was recently added to the longline fleet. This vessel has a steel hull and a refrigerated fish hold, and has an extended cruising range. The vessel began operations in July 1969 and has fished

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[1] NOAA, National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory, Honolulu, Hawaii 96812.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.

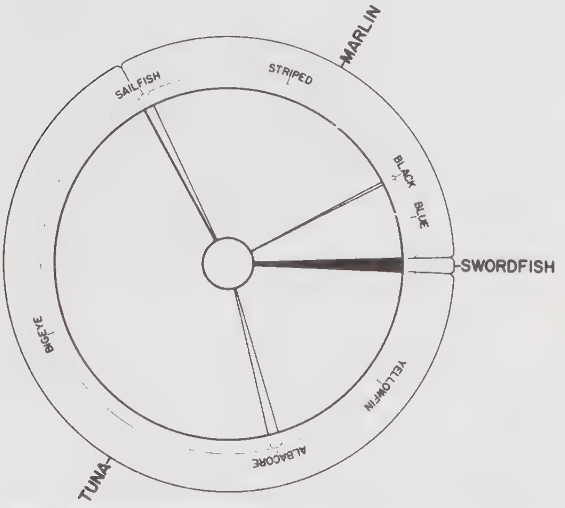
as far as 1,482 km (800 miles) from the Hawaiian Islands (Kanayama, 1970).

Similar to the Japanese longline fisheries, the catches in the Hawaiian longline fishery are made up mostly of large tunas. During the period from 1964 to 1967, considering only the tunas and the billfishes, the tunas, by weight, made up about 66% of the catch, the marlins about 32%, and the swordfish, *Xiphias gladius,* about 1% (Fig. 1). Among the tunas, bigeye tuna dominated the catch followed by yellowfin tuna and albacore, *Thunnus alalunga.* Among the billfishes, striped marlin dominated the catch, followed by blue marlin and swordfish. Small numbers of sailfish, *Istiophorus platypterus,* and shortbill spearfish, *Tetrapturus angustirostris,* are also taken. In 1970, the tunas and billfishes landed by the longline fishery were valued to the fishermen at $1,311,471. The billfishes contributed $291,837 (22%) to this amount.

Other species taken on the longline, in their order of importance, are dolphin or mahimahi, *Coryphaena hippurus:* wahoo, *Acanthocybium solandri;* and a few skipjack tuna, *Katsuwonus pelamis.*

LANDINGS OF STRIPED MARLIN AND BLUE MARLIN

The annual landings of blue marlin ranged between 47 and 366 metric tons during the period from 1952 to 1970 (Fig. 2). The landings declined steadily from a high of 366 metric tons in 1954 to a low point of 48 metric tons in 1968. The landings recovered a little in 1969 and 1970.



CATCH COMPOSITION (BY WEIGHT) OF HAWAIIAN LONGLINE FISHERY

Figure 1.—Composition of the tuna and billfish landings in the Hawaiian longline fishery.

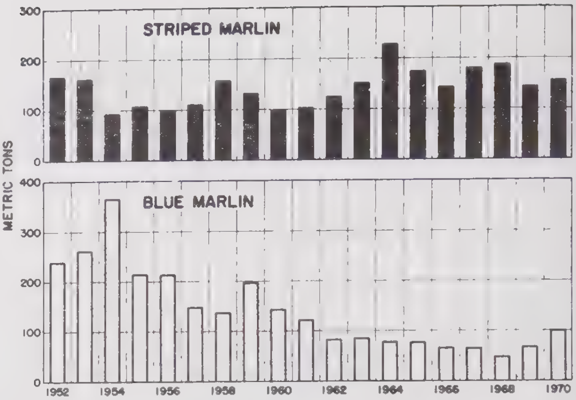


Figure 2.—Annual landings of blue marlin and striped marlin from 1952 to 1970 in Hawaii.

The annual landings of striped marlin fluctuated between 93 and 228 metric tons during this same period (Fig. 2). No clear trends are evident in the landings although it appears that the landings between 1963 and 1970 were slightly higher than the landings prior to 1963. Of interest is the change in dominance from blue marlin to striped marlin in the landings beginning in 1962. This change was caused primarily by the declining blue marlin catches.

Strasburg (1970) presented data on the monthly landings of blue marlin and striped marlin in the Hawaiian fishery from 1950 to 1963. For the period 1950 to 1960, Strasburg noted a complementary nature in the landings of the two species in that striped marlin were caught in large numbers when the blue marlin catches were lowest and vice versa. He noted, however, that the landing peaks of the two species tended to coincide in 1961 and 1962. Monthly landings from 1963 to 1970, however, again showed a displacement in peak landings for striped marlin and blue marlin (Fig. 3). Blue marlin catches were highest in summer and lowest in winter, whereas striped marlin were more abundant in the winter than in the summer. The striped marlin landings were also characterized by having more than one peak in a year, and by wide fluctuations from month to month. The biggest dip in the landings each year usually occurred in the third quarter.

Of interest is a similar complementary nature in the catches of yellowfin tuna and bigeye tuna in the Hawaiian longline fishery. The peak catches of yellowfin tuna are made during the summer while good catches of bigeye tuna are made during the winter and spring (June, 1950; Otsu, 1954; Shomura, 1959). This suggests that striped marlin and bigeye tuna may be responding to a different set of environmental factors from the blue marlin and yellowfin tuna. Strasburg (1970) has suggested a relation to the food supply to explain the complementary abundance of striped marlin and blue marlin around Hawaii. He noted that blue marlin fed largely on skipjack tuna, which were more abundant in the summer. This may account for the larger numbers of blue marlin during the summer.

Further evidence that the blue marlin are indeed responding to the presence of their prey can be seen in the relation between the landings of skipjack tuna and blue marlin in Hawaii (Fig. 4). Generally speaking, good catches of blue marlin corresponded to good catches of skipjack tuna. The situation in 1965, however, did not conform to the general trend. The reason for this is not known.

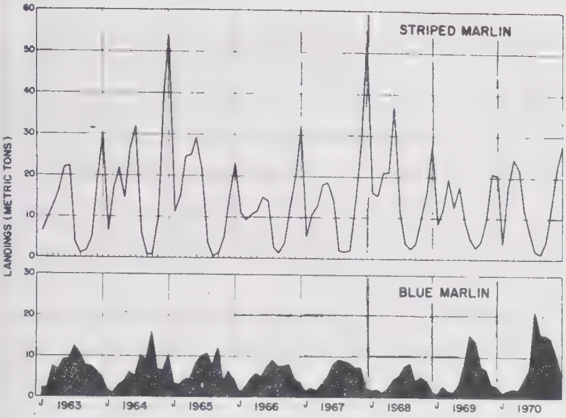


Figure 3.—Monthly landings of blue marlin and striped marlin from 1963 to 1970 in Hawaii.

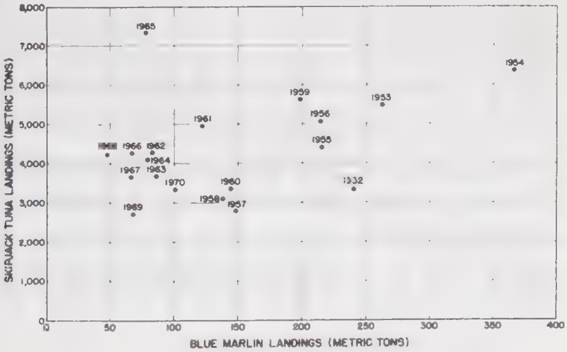


Figure 4.—Relation between landings of skipjack tuna and blue marlin in Hawaii.

CATCH PER UNIT OF EFFORT

The CPUE (catch per unit of effort) for striped marlin and blue marlin was determined to see if CPUE had any effect on the monthly landings. As Shomura (1959) indicated, measures of effort such as number of hooks or baskets of gear fished, are not readily available for the Hawaiian longline fishery. Thus for his analysis of the abundance of tunas around Hawaii, he used the number of trips as a measure of effort. Following Shomura, the number of trips was used to calculate CPUE, here given as number of fish caught per trip on a monthly basis (Fig. 5).

The catch rates for striped marlin and blue marlin showed the same trends as the monthly landings. Similar to the monthly landings blue marlin catch rates usually peaked from July to September. During the period from 1961 to 1969, however, the annual summer peak in the catch rates has shown a small but steady decline.

Similarly, the monthly catch rates of striped marlin showed the same trends, although the fluctuations were not as pronounced as the monthly landings. As did the monthly landings, the monthly catch rates for striped marlin showed two peaks annually, usually one in the spring and the other in the fall. In contrast to the blue marlin, the annual peaks in the monthly catch rates for striped marlin from 1961 to 1969 have increased slightly.

SIZE OF FISH

The quarterly weight-frequency distribution of striped marlin by sex is shown in Figure 6. The size

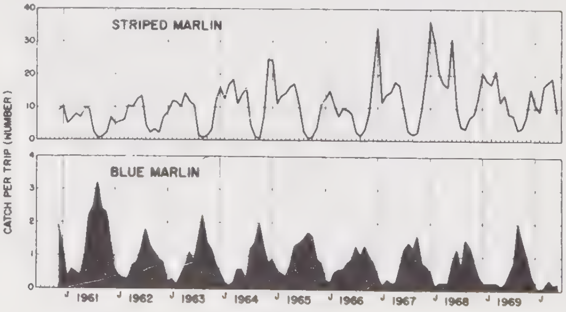


Figure 5.—Monthly catch per trip of blue marlin and striped marlin.

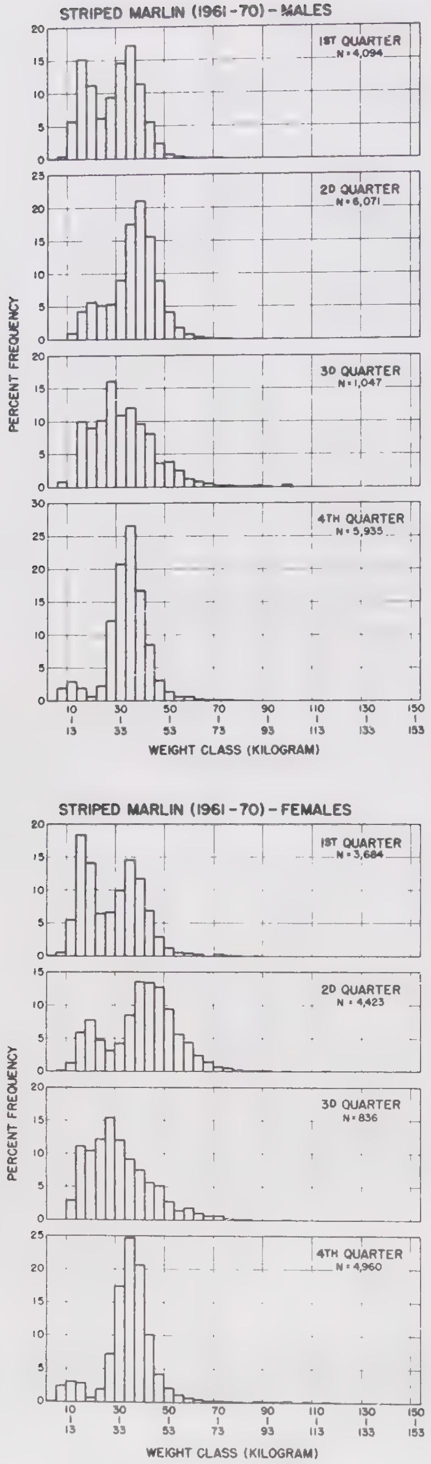


Figure 6.—Weight-frequency distribution of striped marlin.

of male and female striped marlin are about identical and the size-frequency distribution of the males and females show almost no difference. They ranged from 3 to 147 kg (7 to 324 lb). It is interesting that during the first, second, and fourth quarters, the size-frequency distribution shows a bimodal distribution while in the third quarter the size distribution only shows one mode. In the first quarter the modes are located between 14 and 18 kg (31 and 40 lb) and 34 and 38 kg (75 and 84 lb), in the second quarter between 18 and 22 kg (31 and 48 lb) and 38 and 46 kg (84 and 101 lb), and in the fourth quarter between 10 and 14 kg (22 and 31 lb) and 34 and 38 kg (75 and 84 lb). In the third quarter the single mode is located between 26 and 30 kg (57 and 66 lb).

It was noted earlier that the monthly landings showed greater fluctuations than the monthly catch rates and that the biggest dip in the landings was found consistently during the third quarter. This was apparently caused by a combination of low catch rates and the presence of only intermediate size fish in the landings in the third quarter. In the third quarter striped marlin represented by the larger of the two modes found in the other three quarters are evidently not present in large numbers in Hawaiian waters.

Of interest is the observation that larvae of striped marlin are not found in Hawaiian waters (Matsumoto and Kazama, 1974). Matsumoto and Kazama have suggested several reasons for the absence of striped marlin larvae, including the possibility that adult striped marlin leave Hawaiian waters to spawn elsewhere. They cite as evidence the absence of the larger size group of striped marlin in the Hawaiian Islands area starting in about July. As noted above, my data show that the larger striped marlin are not present in the commercial landings in large numbers in the third quarter.

In contrast to the striped marlin, the blue marlin show striking differences in size between the sexes and also in their size distribution (Fig. 7). The females grow to be much larger than the males; they ranged from 7 to 444 kg (15 to 979 lb). In the first and fourth quarters no clearly defined modes are present in the female weight-frequency distribution. In the second quarter a single mode is evident between 140 and 144 kg (309 and 317 lb). The third quarter distribution shows a mode between 120 and 184 kg (264 and 406 lb).

The size distributions of the males, on the other hand, show a pronounced mode between 44 and 80 kg (97 and 176 lb) in all quarters of the year. They ranged from 12 to 140 kg (26 to 309 lb).

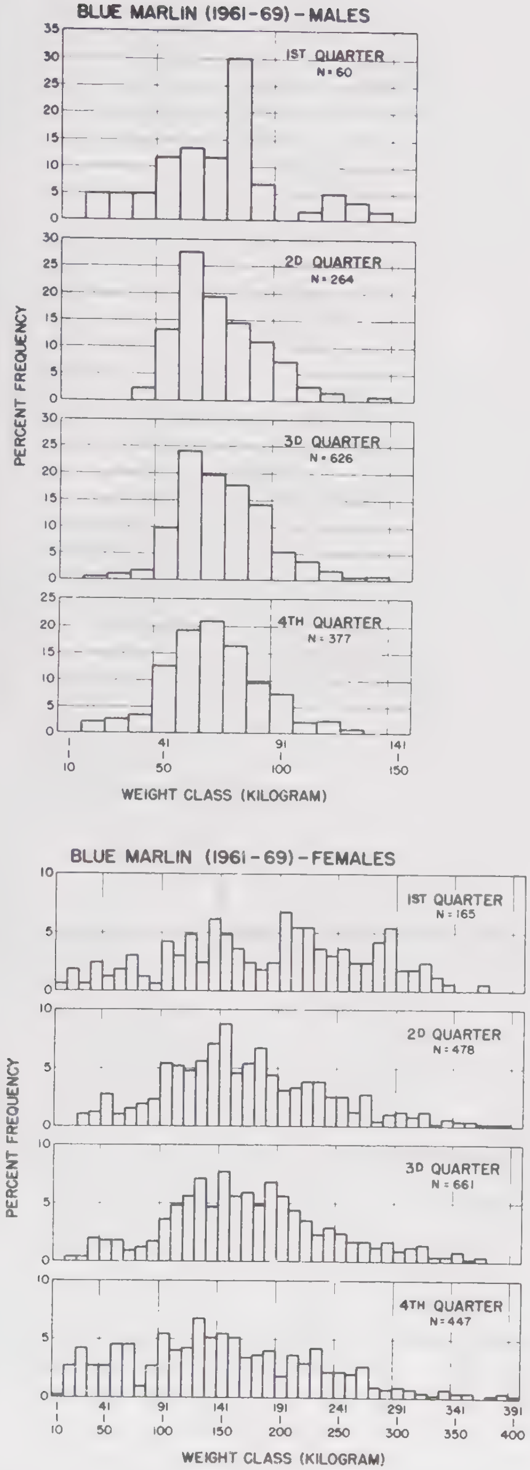


Figure 7.—Weight-frequency distribution of blue marlin.

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Notes on the Tracking of the Pacific Blue Marlin, *Makaira nigricans*

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ABSTRACT

In July of 1971 and 1972 five Pacific blue marlin, *Makaira nigricans*, were tagged with temperature sensing, ultrasonic transmitters off the west coast of Hawaii. These were tracked for durations up to 22½ h. The paths of three showed movement in a northerly direction. The other two showed no movement. Average swimming speed ranged from 2.2 km/h to 3.4 km/h for the three fish tracked. Swimming depths differed considerably among the three.

The Pacific blue marlin, *Makaira nigricans*, found off the Kona coast on the west side of the island of Hawaii has attracted sport fishermen from all over the world. Veteran anglers of that area usually fish where the bottom slopes steeply from 200 to 2,000 m; but movement patterns of this prized fish, if patterns do indeed exist, are unknown.

The Honolulu Laboratory of the National Marine Fisheries Service initiated a project in 1971 to study the movements of the blue marlin using a fish tag that transmitted ultrasonic pulses. The research ship, *Charles H. Gilbert*, tracked one blue marlin during 13-16 July 1971, and four during 24-29 July 1972. Fish were tracked for periods ranging from 1 to 22½ h. Path, depth, and speed of swimming are reported.

MATERIALS AND METHODS

Transmitter and Receiving Equipment

The basic unit of the system is the ultrasonic tag. The tag, cylindrical with faired ends, measures 16.5 cm long and 1.8 cm in diameter (Fig. 1a). It produces a 50 kHz carrier signal with a pulse rate that is a function of the surrounding water temperature. Estimation of depth of fish is then possible. The tags have a temperature range of 7°-27°C, an active life of 10 days, and a reception range of about 1.2 km with the equipment aboard *Charles H. Gilbert*.

The tags are attached to the fish with a leader of fine monel wire rope (0.7 mm diameter). The 25-cm leader is embedded at one end of the tag and crimped to an anchor plate of curved, stainless steel (Fig. lb). The plate is 7.4 by 1.8 cm with a sharpened end. A specially tooled rod at the end of 2½ m pole (Fig. 1c) is used to force the anchor plate into the back of the marlin. The drag of the tag and the curvature of the plate move the plate into position under the skin. The toughness of the skin holds the plate in place.

Ultrasonic signals are received via a hydrophone (Honeywell, model HX-74C[2]) mounted in a well in the hull of *Charles H. Gilbert* and a low-frequency receiver (Lawson) mounted on the bridge. Pulse frequency is determined by visually displaying output signals on a storage oscilloscope (Tektronix, model 564). Sensitivity of the hydrophone to 50 kHz transmission is minus 70 db volt/microbar. The cone-shaped beam of the hydrophone has a width of 25° at the minus 3 db level. The hydrophone can be rotated horizontally 125° on both sides of the bow and vertically 90° by electric scan motors controlled by the tracker on the bridge.

Capture and Tagging of Blue Marlin

Bart Miller and his sport fishing boat, *Christel*, (Kona, Hawaii) were engaged to catch and tag marlins. Fish were caught by trolling. As soon as a marlin struck, the line was pulled in by hand to bring

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[1] NOAA, National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory, Honolulu, HI 96812.

[2] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

FROM Shomura, R. S., and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972. Part 2. Review and contributed papers. NOAA Technical Report NMFS SSRF-675, 1974.

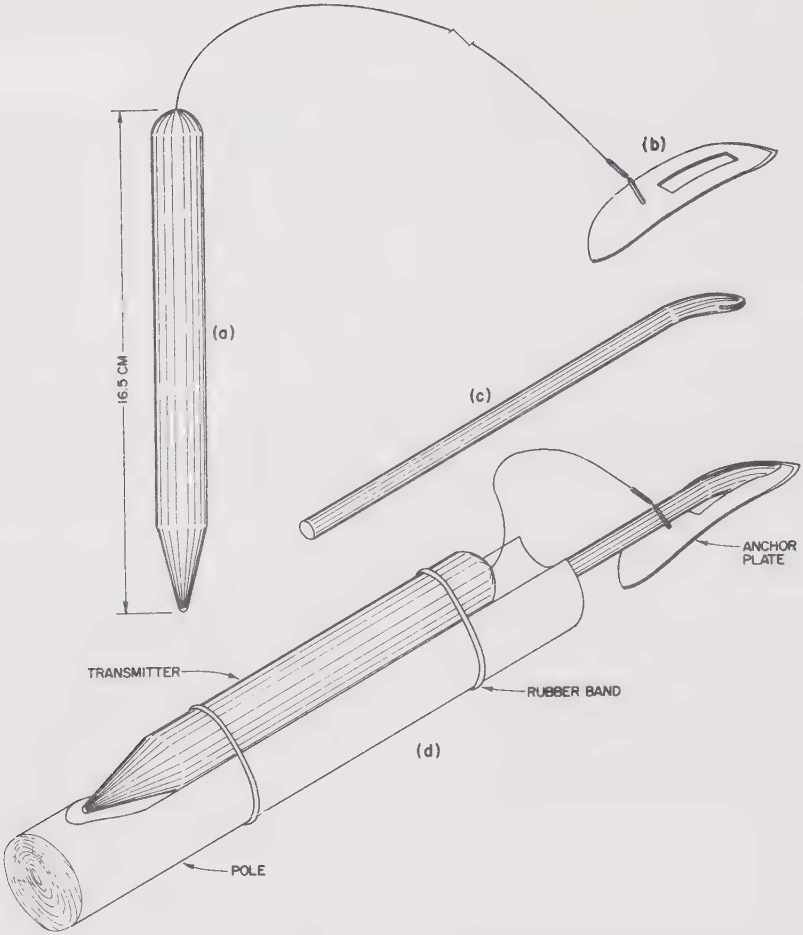


Figure 1.—Ultrasonic transmitter and tagging apparatus. **a.** Temperature sensing transmitter. **b.** Anchor plate. **c.** Rod for applying anchor plate. **d.** All items assembled.

the fish alongside as quickly as possible. When the fish was alongside the boat, its condition was checked and its size was estimated. If the fish appeared to be in good condition, the tag was inserted and the fishing line was cut to release the fish.

Many of the people of the sportfishing community took an active interest in the tracking project. As a result several fishermen offered to donate their marlins. Upon receiving radio communication that a fisherman was willing to donate a hooked marlin, *Christel* transferred the tag, harpoon, and sometimes a crew member. Tagging operations on the other boats were similar to those aboard *Christel*.

Tracking Procedures

During the catching and tagging operation *Charles H. Gilbert* was positioned 200-300 m away from the fishing boat. Upon release of the fish, the following data were recorded at 5-min intervals: time, ship's heading, relative bearing of the hydrophone, tilt angle of the hydrophone, and pulse rate of the tag. Ship's position was determined and recorded at half-hour intervals. Because of poor signal-to-noise ratios, it was not always possible to measure the pulse rate. Because of a malfunction in the tilt angle indicator during the 1972 operations, the observer was sure of the tilt angle only when the hydrophone was at 0° or 90°.

The ship was guided to maintain a distance of approximately 800 m from the estimated position of the tagged marlin. Actual distance between ship and fish continually varied from about 400 to 1,200 m for the following reasons: (1) the minimum forward speed of the ship was 4 knots; (2) the ship was not permitted to go astern because the cavitation bubbles from the propeller would completely block the tag signals; (3) the distance between tag and ship could only be estimated from the strength of the signals from the tag.

A bathythermograph cast was made every 4 h to obtain temperature-depth profiles. These profiles and the temperature-dependent pulse rates of the tags enabled estimation of swimming depth of the marlin.

RESULTS

Five blue marlin were tagged and tracked, one on 14-15 July 1971 and four between 25 and 28 July 1972. Dates, size of fish, duration of tracking and remarks on each fish are listed in Table 1.

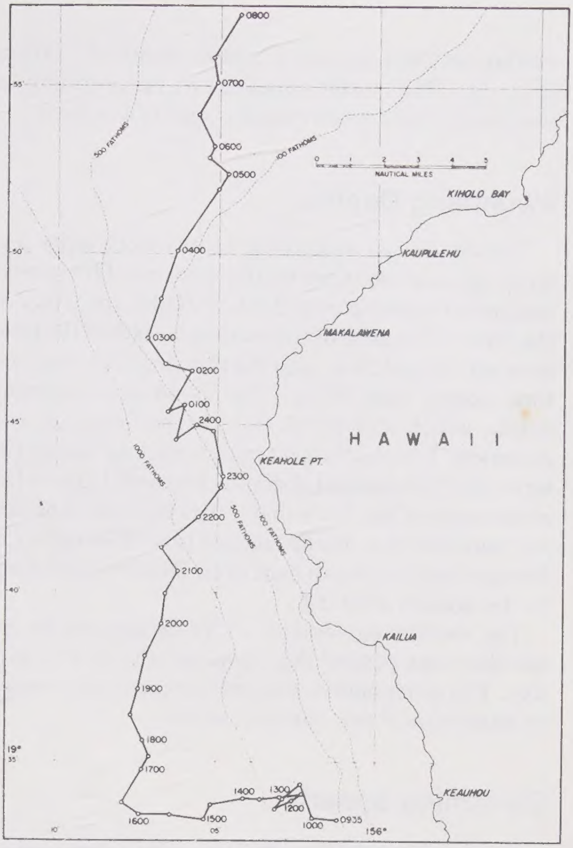
The first tagged marlin was tracked for 22 h 25 min before an equipment breakdown forced a stop. The second fish was in doubtful condition when released. It was difficult to track and contact with it was lost after an hour. The third marlin was tracked for 5 h 22 min before it was lost because of a tactical error. Marlin #4 was abandoned after 7 h because it remained stationary on the bottom soon after it was tagged. After 2 h of swimming the fifth marlin also went to the bottom.

Path

The paths of the marlin tracked are shown in Figures 2 and 3. The path of the last marlin is, of course, of questionable value as the fish lived only 2 h after being tagged. A feature that stands out is that all three marlin moved in a northerly direction. North of Keahole Point there is only one instance where the

Table 1.—Data on blue marlin tagged.

Marlin No.	Estimated weight	Date tagged	Duration tracked	Remarks
	kg (lb)		*h*	
1	270 (600)	7/14/71	22½	Lost—equipment failure.
2	225 (500)	7/25/72	1	Lost—no movement.
3	135 (300)	7/25/72	5½	Lost—tactical error.
4	160 (350)	7/27/72	7½	Abandoned—no movement.
5	70 (150)	7/28/72	8	Abandoned—no movement after 2 h.


0800
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1200
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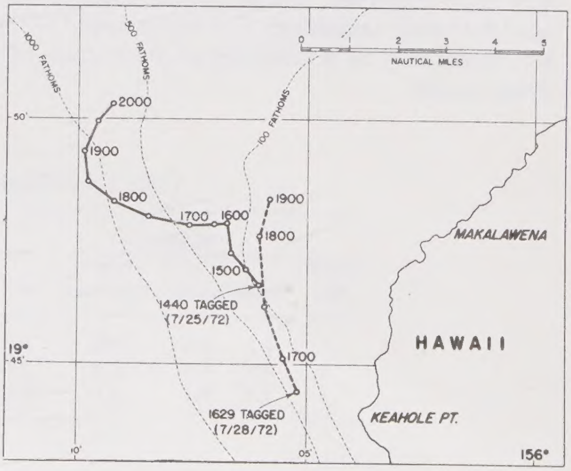
0935
55'
50'
45'
40'
19° 35
10'
05
156°
500 FATHOMS
1000 FATHOMS
100 FATHOMS
0 1 2 3 4 5
NAUTICAL MILES
KIHOLO BAY
KAUPULEHU
MAKALAWENA
H A W A I I
KEAHOLE PT
KAILUA
KEAUHOU

Figure 2.—Path of blue marlin tracked in 1971. Numbers along track denote hour of day.


1000 FATHOMS
500 FATHOMS
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0 1 2 3 4 5
NAUTICAL MILES
50'
2000
1900
1800
1700
1600
1500
1440 TAGGED (7/25/72)
1900
1800
1700
1629 TAGGED (7/28/72)
19° 45'
10'
05'
156°
MAKALAWENA
HAWAII
KEAHOLE PT.

Figure 3.—Path of two blue marlin tracked in 1972. Numbers along track denote hour of day.

marlin ventured beyond a bottom depth of 2,000 m (Fig. 3). This marlin appeared to be returning to shallower water when contact with it was lost.

Swimming Depths

The choices of swimming depths were quite different among the three marlin tracked. The largest marlin (#1), estimated at 270 kg (600 lb), spent half of the time within 10 m of the surface, a sixth of the time between 10 and 30 m, and the remaining third of the time deeper than 30 m. The maximum swimming depth, which was 80 m, was reached only on one occasion. The next largest marlin tracked (about 135 kg or 300 lb) remained at depths between 115 and 185 m throughout the 5½ h that it was tracked. The last and smallest blue marlin tracked (about 70 kg or 150 lb) remained in a depth zone of 60-85 m before it went to the bottom after 2 h.

The vertical movements of the largest marlin did not show any pattern that could be related to time of day. The other marlin were not tracked long enough to determine if any pattern existed.

Swimming Speeds

Swimming speeds of the three marlin were calculated based on the distance traveled every half hour. Results are in Table 2. The average swimming speed of the last marlin is high compared with the others especially in terms of body lengths per second. Marlin #1 and #3 had an average swimming speed of 0.23 body length/sec. Marlin #5, in contrast, averaged 0.45 body length/sec. The higher speed of the last marlin may be a reflection of the distress of a dying marlin.

The maximum for the largest (#1) and the smallest fish (#5) were 0.62 and 0.68 body length/sec compared with 0.32 body length/sec for marlin #3. The two larger marlin (#1 and #3) both had minimum speeds of 0.09 body length/sec while the minimum speed of the smallest was 0.19 body length/sec.

DISCUSSION

A counterclockwise eddy west of the northern half of the island of Hawaii persists there most of the time (R. A. Barkley, pers. comm.). The area of our marlin tracking coincides with that part of the eddy which flows northward. The fact that all three marlin tracked exhibited a northerly movement suggests the possibility that the blue marlin orients or drifts with currents.

One of the problems in tracking marlin is getting one that will survive the trauma of being caught. Of the five marlin tagged two died and one probably died. Three others were caught and not tagged because of their poor condition. To enhance the probabilities of success in marlin tracking, consideration should be given to ways of attaching the tag without catching the fish.

ACKNOWLEDGMENT

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Table 2.—Swimming speeds of blue marlin.

Marlin No.	Minimum			Maximum			Average		
	km/h	knots	body-length/sec	km/h	knots	body-length/sec	km/h	knots	body-length/sec
1	1.1	0.6	0.09	8.2	4.4	0.62	3.0	1.6	0.23
3	0.9	0.5	0.09	3.1	1.7	0.32	2.2	1.2	0.23
5	1.5	0.8	0.19	5.4	2.9	0.68	3.4	1.9	0.45